Part 1. Centers of Origins of Crop Plants and Agriculture

Back to Vavilov: Why Were Plants Domesticated in Some Areas and Not in Others? - J.G. Hawkes

Behind this rather simplistic title of my paper lie a number of problems - some clearly answerable without much difficulty, and others which are not yet answered and perhaps never will be.

We as biologists, ethnologists and geneticists pay tribute to the genius of Nicolay Ivanovich Vavilov - his enormous width of understanding and innovative vision. We may well consider him to be the 'Darwin of the 20th century' with just as enquiring a mind and capacity to recognize the basic similarities between several apparently quite distinct phenomena as Darwin had done in the 19th century.

Whereas Darwin (1868) studied the diversity of all living organisms known to science, Vavilov directed his vision toward domesticated plants just as had Alphonse de Candolle (1882) before him. Clearly, Vavilov's depth of enquiry was much greater than that of de Candolle, to whom he pays tribute.

Vavilov was basically a geneticist and plant breeder, approaching the problems of cultivated plant species in terms of the diversity within and between them that might be put to practical ends. For this reason Vavilov was not particularly interested in diversity as such, but only in the diversity that could be put to practical advantage.

If we consider the world flora, even a quick survey will show us that there are many areas of plant diversity which have little to do with cultivated plant origins. Thus, the 'fynbos' plant formation on the very southernmost tip of South Africa is extremely diverse. In quite a small area one can find hundreds of species in quite distinct genera and even plant families. These are very attractive and colorful but were never brought into cultivation by the indigenous people. They were not at all edible and are known today as beautiful and extraordinary examples of plant evolution. A rather similar flora exists in southern Australia, and again, none of its species was brought into cultivation.

To take other examples, let us consider the vast tropical rainforests of South America, Africa and Asia. These differ from the fynbos in that many plants have been used, perhaps for millennia, for food, medicine, clothing and in some instances building materials. But were any of these domesticated? Perhaps a few, such as cassava, pineapple, peanuts, etc., but these were plants from the drier forest margins, and occurred only in certain regions. Several nuts and fruits were gathered for food. They were gathered, eaten and used in a variety of ways. Again, the vastly rich fruit-tree floras of South East Asia were of immense value to the people of such areas but their actual cultivation is comparatively recent.

Let us look at another example, namely the wild spring bulb flora of the central and southern European mountains. These plant communities are very diverse and extremely beautiful, with their bulbs, annuals, shrubs and trees. Few were eaten by humans - in fact the plants themselves had developed mechanisms to prevent their being eaten, such as poisonous or bitter roots, bulbs, etc. and spiny leaves and branches. None of these was domesticated in ancient times.

Much further north in northern Europe and the steppes of Asia, as well as the northern part of North America and the southern part of South America, the species diversity diminishes very greatly. There are only a few species able to survive, grazed by wild and domesticated cattle, but these are not of direct use to humans as food, only through their horses and cattle.

We thus have a curious paradox; namely, that there is considerable wild plant diversity up to about 45-50°N latitude in Europe, Asia and North America, and southward to 35-40°S latitude in the southern continents, apart from desert and semi-desert areas. However, only in certain areas between 45°N and 30°S latitudes were potential crop plants actually domesticated. This problem was not really solved by Vavilov, or by his predecessor de Candolle and others. Why was only part of the world's plant diversity domesticated?

Vavilov noted that the centers of origin of cultivated plants occurred mostly in mountainous regions between the Tropic of Capricorn (23°28') south of the equator and about 45°N of the equator in the Old World. In the New World crop domestication occurred between the two tropics (Cancer and Capricorn) approximately. In all cases agricultural origins and primitive diversity occurred in high and complex mountain regions. Why only these?

Let us now return to the process of domestication. How did plants become domesticated despite their evolutionary processes to protect them from being eaten by the development of various defensive mechanisms such as poisons, bitter substances, etc.? One strategy of survival adopted by many plants is to produce so many seeds that even if most of them are eaten enough will remain to provide for the next generation. And the plants that do this superbly well are grasses. To a lesser extent those that do this quite well are herbaceous legumes. This, then, may be the solution to the problem of how humans began the process of domestication. Hunter-gatherers took and ate the natural surplus and left enough seeds (probably by chance) to provide for the next generation. Later, when non-shattering mutants occurred by chance, these were adopted automatically by the primitive farmers. From this point evolution under domestication began to take place.

As far as can be seen from the literature, Vavilov did not consider these points in any detail. What he did do - and that superbly well - was to pinpoint the exact areas where crop plant diversity showed us the centers of origin of world crops.

Vavilov considered that "as a rule the primary foci of crop origins were in mountainous regions, characterized by the presence of dominant alleles." In his work entitled *The Phytogeographical Basis for Plant Breeding* (Vavilov 1935) he summarizes and pulls together all his previous work on centers of origin and diversity. In this he recognizes eight primary centers, as follows.

I. The Chinese Center - in which he recognizes 138 distinct species of which probably the earlier and most important were cereals, buckwheats and legumes.

II. The Indian Center (including the entire subcontinent) - based originally on rice, millets and legumes, with a total of 117 species.

IIa. The Indo-Malayan Center (including Indonesia, Philippines, etc.) - with root crops (*Dioscorea* spp., *Tacca*, etc.) preponderant, also with fruit crops, sugarcane, spices, etc., some 55 species.

III. The Inner Asiatic Center (Tadjikistan, Uzbekistan, etc.) - with wheats, rye and many herbaceous legumes, as well as seed-sown root crops and fruits, some 42 species.

IV. Asia Minor (including Transcaucasia, Iran and Turkmenistan) - with more wheats, rye, oats, seed and forage legumes, fruits, etc., some 83 species.

V. The Mediterranean Center - of more limited importance than the others to the east, but including wheats, barleys, forage plants, vegetables and fruits -especially also spices and ethereal oil plants, some 84 species.

VI. The Abyssinian (now Ethiopian) Center - of lesser importance, mostly a refuge of crops from other regions, especially wheats and barleys, local grains, spices, etc., some 38 species.

VII. The South Mexican and Central American Center - important for maize, *Phaseolus* and Cucurbitaceous species, with spices, fruits and fibre plants, some 49 species.

VIII. South America Andes region (Bolivia, Peru, Ecuador) - important for potatoes, other root crops, grain crops of the Andes, vegetables, spices and fruits, as well as drugs (cocaine, quinine, tobacco, etc.), some 45 species.

VIIIa. The Chilean Center - only four species - outside the main area of crop domestication, and one of these (*Solarium tuberosum*) derived from the Andean center in any case. This could hardly be compared with the eight main centers.

VIIIb. Brazilian-Paraguayan Center - again outside the main centers with only 13 species, though *Manihot* (cassava) and *Arachis* (peanut) are of considerable importance; others such as pineapple, *Hevea* rubber, *Theobroma cacao* were probably domesticated much later.

After this brief survey it seems quite clear that out of the very wide range of plant diversity in the tropical and warm temperate regions of the world our major food crops have come mainly from high mountain valleys, isolated from each other to a large extent and with a very great habitat range. Here people made selections of wheat, barley, oats, rye, potatoes and maize which were eventually cultivated.

These plants were weeds or possessed the syndrome of not being able to compete well with climax vegetation. Hence they grew in areas where nature or humans had reduced competition from other species, were noticed, eaten, resown by chance and eventually became domesticated. Several other weedy plants were never or only temporarily domesticated, remaining as weeds but often hybridizing by chance with the cultivated ones and thus enhancing their diversity.

It seems that the restricted access of the mountain valleys and the wide range of altitudes helped to produce and select the diversity needed for domestication. Similar selection pressures even in unrelated crops produced similar types of adaptation, a process developed by Vavilov into his Law of Homologous Series. Because such adaptation in only partially related crops must surely have been due to mutations on distinct loci in each crop, this writer feels that a more correct title might have been the Law of Analogous Series. However, the phrase has persisted as Homologous Series and we must retain it as just one of the extraordinarily innovative ideas put forward by the great genius, N.I. Vavilov.

<div align="center">Conclusions</div>

In this brief review of the history of plant domestication we can see clearly that it took place mainly in mountainous regions more or less within or near the tropics. It is still difficult to understand why it took place in those regions and nowhere else, when plant diversity elsewhere was so high. While not proposing to give a final answer, I believe the following points are relevant.

First, we can eliminate areas such as the 'fynbos' of South Africa where there was little or no production of starchy seeds or tubers for the people to eat.

Second, we have to consider the vast resources of tropical forests. In these it seems that there were no processes leading to domestication, since abundant food was there to be gathered in the form of fruits, nuts and starchy tubers throughout the year.

Third, we must consider the areas of the southern European plains and mountains with abundant ornamentals, and some seeds and bulbs for gathering, but probably not enough to provide food throughout the year.

Fourth, we have the high mountain areas mainly between the Tropics of Cancer and Capricorn. These areas are seasonal in climate, with a wide range of temperature and rainfall due to differences of altitude and aspect. Here were closed ecological systems of grasses and legumes where mutant forms could thrive and become established. Here also were isolated human communities exerting their own selection pressures for larger seed size, adaptation to drought, humidity and extremes of climate. These were ideal conditions for mutations and selections, especially for large seed size and adaptation to environmental extremes.

Weedy relatives of the crops were also present, adding to the genetic diversity by random mating with the primitive crops themselves. In the crop I know best -potatoes - one can find not only a range of ploidy, from diploid to pentaploid, but clear evidence for crosses between weed species and cultivated ones as well as the natural introduction of frost resistance from wild species into the cultivated ones.

To sum up, it seems clear to me that evolution of domesticates is very much promoted by the factors of varied microclimate, aspect, altitude, restricted habitats and human selection which are all present in the intertropical mountain zones of the Old and New Worlds. Such a wide range of natural and human selection pressures is not available to the same degree of intensity in other world regions. Vavilov was the first investigator to study and understand these systems and to use them as a basis for present and future plant breeding. At the same time, since Vavilov was not only a geneticist and plant breeder, but also a man of wide interests and intelligence, he was able to provide a theoretical background to interpret crop genetic diversity in all its aspects and thus to make it available for the whole world.

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Vavilov's Theories of Crop Domestication in the Ancient Mediterranean Area - A.A. Filatenko, A. Diederichsen and K. Hammer

Introduction

The papers by Nicolay Ivanovich Vavilov, elucidating the origin and geography of cultivated plants, have served as a systematic collection of such work with plants and its presentation to the world in general. The first fundamental paper by Vavilov, *Centers of origin of cultivated plants,* was dedicated to Alphonse de Candolle, the first person in the history of science to pose questions concerning independent centers of origin (Vavilov 1935). Vavilov's (1920) work on the homologous series was recently re-recognized (Hammer and Schubert 1994) but his work on the centers of origin continues to be discussed (Zhukovsky 1968; Zeven and de Wet 1982; Harris 1990).

Methods used by Vavilov for determining the centers of type-formation (centers of origin) of cultivated plants

For the purpose of establishing the centers of type-formation or the centers of diversity the 'differential phyto-geographical method' was applied (Vavilov 1935). It can be described by the following steps:

1. A strict differentiation of the plants studied into Linnaean species and intraspecific groups by all available means of various disciplines beginning with morphology, agrobotany, phytopathology, cytology and recently by molecular methods.

2. Delimitation of the distribution areas of these plants and, if possible, also of the distribution areas in the remote past when communication and seed exchange were more difficult than at present.

3. A detailed determination of the composition of the varieties and races of each species, and a general system of the genetic variability within the different species.

4. Establishment of the distribution of the genetic variability of the forms of a given species as far as regions and areas are concerned, and the establishment of the geographical centers where these varieties are now accumulated. Regions of maximum diversity, usually also including a number of endemic types and characteristics, can also be centers of type-formation.

5. For a more exact definition of the center of origin and type-formation it is necessary to establish the geographical centers of concentrations of species that are botanically closely related as well.

6. Finally, the establishment of the areas of diversity of wild subspecies and species that are closely related to the cultivated species in question should be used for amendment and addition to the area defined as area of origin, when the differential method for studying races is applied to them.

Vavilov's original concepts

In 1940 Vavilov stated that the method of differential taxonomy offers an opportunity to trace the dispersal of many cultivated plants. It demonstrates their stages of evolution with respect to both the initial origin and their introduction into cultivation within different areas. It shows their relation to wild subspecies and species, but also demonstrates the subsequent evolution under domestication of these plants when dispersed from the basic centers and undergoing changes under new conditions and the further effects of natural and artificial selection.

The studies of the origin of different cultivated plants led Vavilov to the establishment of new concepts, i.e. primary and more ancient crops in contrast to secondary ones, allowing him to characterize with good precision the centers where agriculture originated and the pathways along which it was dispersed.

The study of the laws of the geographical distribution of plant resources on earth and the establishment of the enormous infraspecific diversity of the majority of crops allowed not only a determination of their localization but also offered an opportunity to ascertain the period of origin of the plants most important for cultivation. In 1924 Vavilov wrote: "The history and origin of human civilizations and agriculture are, no doubt, much older than what any ancient documentation in the form of objects, inscriptions and bas-reliefs reveals to us. A more intimate knowledge of cultivated plants and their differentiation into geographical groups helps us attribute their origin to very remote epochs, where 5000 to 10,000 years represent but a short moment" (Vavilov 1992).

The number of centers listed in Vavilov's papers increased dramatically during a comparatively short period from three in 1924 to five during 1926, six in 1929, seven in 1931 and eight in 1935, but was again reduced to seven in 1940. Each publication appeared to be the result of consideration of additional data (Vavilov 1924, 1929, 1931, 1932, 1935, 1938, 1940).

In 1932, Vavilov wrote: "Many historical problems can be understood only because of the interaction between man, animals and plants." Centers differ with respect to the concentration of specific variation. Vavilov attached great importance to data indicating regions of major concentration of specific and generic variation. During the arrangement of these regions according to the richness of cultivated floras, the Chinese center was put in first place and the Hindustani one in second (Vavilov 1934). More recent data (1940) led to the necessity for changing these places: 33% of all cultivated plant species are to be found concentrated in the southern Asiatic tropical center, which at Vavilov's time nourished up to one-fourth (now one-third) of the population of the world. In eastern Asia, the second most important center, 20% of the number of species of cultivated plants are grown. As far as the number of species introduced into cultivation is concerned, southwestern Asia follows with 14%. However, Vavilov attached a particular importance to that center since the composition of what is cultivated in the territory of Russia is a consequence of the influence from Asia in general and specifically from Asia Minor in a wide sense and Inner Asia. He determined the boundaries of that center.

In the papers published in 1934 and 1935, the division of southwestern Asia into two centers is suggested: the Middle Asian one and one covering Asia Minor. In 1937, the Middle Asian center was renamed the Inner Asian one. It belongs to one of the five major regions where cultivated plants originated in Asia and includes northwestern India, Afghanistan and the mountainous parts of Turkistan (Uzbekistan, Tajikstan and a part of Turkmenistan). This name, however, does not agree with the centers of origin or with their subdivision in Vavilov's later papers. Its appearance is explained by the fact that during that period and until recently, the exact spatial-geographical borders of Inner Asia

had not been clearly outlined (Grach 1984).

After rejecting the division of the southwestern Asiatic center, Vavilov (1938, 1940) discussed the composition of the complex of species formed by cultivated plants within the territory in question. He refers to the close relationship between Cis-Caucasus and Asia Minor: "An enormous potential of species and even of genera is concentrated there, constituting genetically distinct units" (Vavilov 1938). In addition to quantitative characteristics, Vavilov concentrated his attention on the specific composition of cultivated plants for each of which endemic genera, species and even forms occurred.

Vavilov used equally the terms 'center', 'focus' and also 'area' of origin. Their definition is important: the geographical centers are basic and independent foci where agricultural crops originated but are also geographic areas where cultivated plants are grown. Passing from one of Vavilov's papers to another concerning the problem of the origin of cultivated plants, it is possible to conclude that the terms 'center' and 'focus' are mainly associated with large territories. In his last papers, he writes about 'areas of basic origin of cultivated plants' and about the conventional concept of 'center of origin' such as suggested by Darwin.

Summing up the data concerning the hundreds of cultivated plants from all over the world resulting from the systematic collection by the All-Union Institute of Plant Industry (VIR), Vavilov wrote in 1935: "We can now speak with a considerably greater accuracy than dreamed of ten years ago about the eight ancient and basic centers of agriculture in the world, or, more accurately about the eight independent areas where plants were initially taken into cultivation."

E.N. Sinskaya's approach

After Vavilov's untimely death in Saratov in 1943, Sinskaya continued his work concerning the establishment of borders for the centers of cultivated plants and for the specification of the relationship between the centers (areas).

Sinskaya noted that several amendments can be made to Vavilov's theories concerning the centers of origin of cultivated plants but they amount only to a correction of details. "The basic composition of cultivated plants, typical of this or that center, remains stable" (Sinskaya 1966).

As far as the historical character of Vavilov's works toward the establishment of the centers of agricultural crops is concerned, Sinskaya calls our attention to the prevalent use of the expressions "historical-geographical area" or "geographical areas of the historic development of a cultivated flora" which appear regularly in Vavilov's papers from 1924 to 1940 (see also Karpyceva and Sokolova 1987).

Sinskaya elaborated a more detailed approach to the analysis of the cultivated plants in their centers of origin. This approach is based on a differentiated characterization of the endemism the various taxa have in a given area which are divided into the following categories:

- genera originating from the area

- genera having one of their centers of origin or their most important secondary center of origin in the given area

- species strictly endemic for the given area

- species endemic to the given area, but having their first origin in another area

- species having one of their centres of origin or their most important secondary centre of origin in the given area.

Sinskaya (1969) gave examples for the main categories and proposed to differentiate five basic geographical areas of historical development of cultivated plants, each having its subareas. The basic geographical areas of origin of cultivated plants after Sinskaya are shown in Figure 1 and Table 1. For all subareas Sinskaya (1969) lists the respective cultivated plants together with their characterization by the above-named categories.

The development of important genera (such as *Triticum, Secale, Hordeum, Beta, Brassica, Daucus, Lens, Linum, Olea, Mandragora, Pisum, Melilotus* and many others), which include the major proportion of all crops, forms the basis for agricultural production in countries around the Mediterranean, but most of them are intensively grown in Asia as well as in Southwest Asia. Phytogeographical studies have revealed that compared with the areas of Africa south of the Mediterranean, there is a characteristic cultivated flora that is not less rich than those in other centers where agriculture arose. Many cultivated plants have undergone very old but secondary development there, e.g. in Ethiopia.

While further developing Vavilov's ideas about the centers of origin, Sinskaya (1966) singled out the African region for the historic development of cultivated flora. Ancient Mediterranean elements (actually both Mediterranean and Southwest Asiatic ones) predominated in the composition of the cultivated flora of Ethiopia but are not sharply delimited from those of other African areas. Elements from South Asia also occur there.

This area is rather an area of introduction than of distribution of cultivated plants to other places. Sinskaya (1966, 1969) calls such territories "dependent areas", to which belong not only Ethiopia, but also North America, where agriculture developed on the basis of Mexican and Central American crops and, later on, that of crops from the Old World. In central and northern Europe, on the Russian steppes and in Siberia, agriculture is based primarily also on cultivated plants, introduced from the subareas Southwest Asia and Mediterranean, etc. The agriculture of the "dependent areas" underwent a certain period of development and, therefore, is not limited, judging by the large quantity of plants introduced into cultivation from less rich, wild flora of these territories.

During his work on the question of the origin of cultivated plants Vavilov himself only once used the term 'gene-center'. It was for his lecture at the International Congress of Genetics at Berlin in 1927. This term, however, is often used today possibly because it is easy to pronounce. Nevertheless the name 'gene-center' is quite abstract which subsequently gave rise to several misunderstandings of the theory of the centers of origin of cultivated plants. The botanical investigations concerning the centers of origin still continue and the collections gathered are being thoroughly studied at VIR.

Table 1. Geographical areas of historical development of cultivated flora (after Sinskaya 1966, 1969).

Basic areas of origin	Subareas
I. Ancient Mediterranean	Southwest Asia 1a. Anterior Asia (Transcaucasus, Asia Minor, Near East, West Iran) 1b. Middle Asia (Turkistan, Afghanistan, East Iran, North West India, Pakistan)

	Mediterranean
II. East Asia	Northeast Asia (Japan, Manchuria) Southeast and Central China
III. South Asia	South China, India and Sri Lanka Malesian
IV. Africa	
V. New World	Central America South America

The origin of cultivated plants, in particular of wheats (*Triticum* L.)

Vavilov referred emphatically to the division of the globe into floristic regions and subregions such as those accepted by conventional phytogeography for elaborating the geographic origin of cultivated plants.

The origin of cultivated wheat is located in the Ancient Mediterranean (syn.=Old Mediterranean) which includes, according to Vavilov's last paper (1940), the Mediterranean region and Southwest Asia. The latter was divided by Vavilov (1935) into Asia Minor in a broader sense and Inner Asia. Sinskaya (1966, 1969) considers these territories as subareas of the Ancient Mediterranean (Tables 1, 2). Many species, genera and families which were responsible for the development of cultivated plants originated from these subareas. Nevertheless, every subarea has its characteristics due to the ecological conditions and the richness of the flora of wild and cultivated plants as well as to the ancient history of agriculture. The area of origin of wheat is Southwest Asia. The greatest amount of endemic species and a huge amount of different intraspecific taxa is found there. The greater the distance from this primary area of origin, the less diversity of the species is observed.

From 26 species of the genus *Triticum* the following species are found in Anterior Asia and are endemic wild plants: *T. urartu, T. araraticum* and *T. dicoccoides.* Endemic cultivated plants are: *T. timopheevii, T. zhukovskyi, T. carthlicum, T. karamyschevii, T. ispahanicum, T. macha, T. vavilovii* and *T. sinskajae. Triticum turanicum* and the wild einkorn *T. boeoticum* mainly occur there. Sinskaya (1969) considers *T. sphaerococcum* a further species, which occurs in northwest India, as an endemic species (Table 2).

A second group of Southwest Asian wheat originated in the Near East subarea but then spread to other areas. They were later replaced, at the beginning of the century, by higher-yielding species and therefore can only be found as relics isolated from each other. They are: *Triticum monococcum, T. dicoccum, T. aethiopicum* and *T. spelta* (Sinskaya 1969; Padulosi *et al.* 1996). These species, which are at present to be found in areas far away from each other, were more intensively developed in other subareas of the Ancient Mediterranean. *Triticum aestivum* and *T. compactum* were intensively developed in Middle Asia and subsequently spread all over the world. *Triticum durum* and *T. turgidum* developed in the more central and western parts of the Ancient Mediterranean, particularly close to the sea coast. East of this area of origin, on the other hand, the process of formation of the further wheat varieties is not observed. A.M. Gorskyi during his expedition to Sinkiang (Western China) found a new endemic wheat named *T. petropavlovskyi* (Dorofeev *et al.* 1979). Vavilov had completed the investigation of Sinkiang in 1929 and regarded this western part of China as one of the geographically most isolated peripheral sites of *Triticum.*

Fig. 1. Geographical regions of development of cultivated flora. Adapted from Sinskaya (1969).

Table 2. Distribution of the species of wheat in the Ancient Mediterranean area of origin of cultivated plants (after Dorofeev *et al.* 1979).

Subarea			Dependent area
Mediterranean [†](147)	**Southwest Asia**		**Ethiopia (250)**[‡]
	Anterior Asia (412)	**Middle Asia (260)**	
T. boeoticum (16)[§]	*T. boeoticum* (57) *T. urartu* (6) *T. araraticum* (13) *T. dicoccoides* (25)		
T. monococcum (13)	*T. monococcum* (14) *T. sinskajae* (1)		
T. dicoccum (7)	*T. dicoccum* (15) *T. ispahanicum* (2) *T. karamyschevii* (3) *T. timopheevii* (4) *T. militinae* (2) *T. zhukovskyi* (1) *T. macha* (14) *T. vavilovii* (7)		*T. dicoccum* (8)[§]
T. spelta (14)	*T. spelta* (14)	*T. spelta* (19)	
T. durum (80)	*T. durum* (75)	*T. durum* (8)	
T. turanicum (4)	*T. turanicum* (34)	*T. turanicum* (7)	
T. turgidum (34)	*T. turgidum* (54) *T. carthlicum* (18)	*T. turgidum* (3) *T. jakubzineri* (1)	
T. polonicum (11)	*T. polonicum* (14) *T. sphaerococcum* (17)	*T. polonicum* (3)	*T. polonicum* (6)
T. compactum (13)	*T. compactum* (40)	*T. compactum* (64)	
T. aestivum (25)	*T. aestivum* (59)	*T. aestivum* (142) *T. petropavlovskyi* (4)	*T. aestivum* (33) *T. aethiopicum* (203)

Number of taxa which occur in the given subarea: [†] number of botanical varieties per area; [§] number of botanical varieties per species.

[‡] Species of wheat, e.g. Ancient Mediterranean elements of northeast African flora.

Table 3. Distribution of taxa of some genera in the Ancient Mediterranean area of origin of cultivated plants.

	Subarea			
	Mediterranean	Southwest Asia		Dependent area
		Anterior Asia	Middle Asia	Ethiopia‡
Hordeum vulgare†				
subsp. *vulgare*	14/3	7	21/3	38/8
subsp. *distichon*	10/1	18/2	7	38/20
Pisum§				
P. formosum	-	1	-	-
P. fulvum	1	1	-	-
P. sativum	8	7	9	-
subsp. *abyssinicum*	-	-	-	1
Beta vulgaris¶	9	5	5	-
Lens††	63/3	-	54/9	2/2

Species of different crops, e.g. Ancient Mediterranean elements of northeast African flora. Number of varieties: † Lukjanova *et al.* 1990; ‡ total/endemic varieties; § Makasheva 1973; ¶ Krasochkin 1960; †† Barulina 1930.

Such peripheral areas were only reached by a few infraspecific varieties of cultivated plants. Nevertheless, Vavilov acknowledged the possibility of finding endemic forms of wheat in these areas. Yue Dahue (1984) also reports findings of *T. petropavlovskyi* by Chinese expeditions to Tibet. *Triticum spelta* was formerly considered a European crop. But *T. spelta* was found in Iran (Kuckuck and Schiemann 1957), in the Transcaucasus (Mustafaev 1961; Dorofeev 1970) and in Middle Asia (Udachin and Shachmedov 1984). This supports the existence of a common Southwest Asia and Mediterranean area of origin.

Other crops

The diversity of barley (*Hordeum vulgare*) is more evenly spread across the Ancient Mediterranean area and several infraspecific taxa are endemic to Ethiopia (see Table 3). The botanical varieties of the genus *Pisum* are also more or less evenly spread in the Ancient Mediterranean area of origin (Table 3).

Several monographs dealing with many different crops have been published by the VIR. Such work is important not only for studies on centers of origin of cultivated plants but also for theoretical and practical agronomy. Such work is the basis for searching for initial material for plant breeding. These monographs are based on: (1) previous publications, (2) a thorough investigation of the accessions of the collection which were not included in previous work, and (3) data obtained through new experimental methods, e.g. physiological, phytopathological, genetical, molecular and other research. But all research done to study plants can only produce useful results if the botanical identification of the material is carried out at the intraspecific level. This rule being basic for scientific work in this field, however, is often neglected.

Taxonomic studies in the tradition of Vavilov, based on the investigation of variation within a species, have also been carried out in Gatersleben (e.g. Mansfeld 1950, 1951; Hanelt 1972; Gladis and Hammer 1992; see Hammer *et al.* 1994).

Recently information on coriander has been provided by Diederichsen (1996). The detailed investigation of the variation of the species *Coriandrum sativum* by several characters caused the author to divide this species into several groups (so far called ecological types), which are connected with the geographical origin in the Ancient Mediterranean area.

The infraspecific classification (Hanelt 1986; Hanelt and Hammer 1995) helps to indicate areas where different types of a given species are to be found. It also is an excellent method to single out and preserve rare accessions in a collection. However in the case of wheat a very interesting group - *T. durum* convar. *villosum* - collected by Vavilov in Syria, Jordan and Lebanon is untraceable in the collection at VIR. It was an extremely xerophytic type with a very hairy ear and similar leaves. A herbarium specimen of it exists at VIR but even that is threatened.

The extinction of durum wheat without ligula (*T. durum* convar. *aglossicon* Flaksb.) from Cyprus was prevented. In its area of origin on Cyprus this type is already extinct. In bulk populations of wheat accessions single plants of this type occurred. Such plants were singled out and received their own number in the VIR catalogue.

In the 1960s and 1970s the landraces collected by VIR staff in the Caucasus comprised more than ten botanical varieties. Of these only one or two are still part of the VIR collection. The VIR collection of Ethiopian wheats has also lost many varieties. Every botanical variety has to be preserved as a single accession, if the original landrace, which contained several varieties, is not reproduced under the conditions which are similar to its natural area of origin (Hammer 1992).

The taxonomical category 'varietas' was introduced by Fr. Alefeld (1866) and Fr. Körnicke (1885) for crop plants and is based on the differentiation by distinct characters. This category makes it possible to orientate quickly and properly in the diversity of a given area. At the same time such classification delivers clear information for the given species with respect to the Law of Homologous Series in variation (Vavilov 1920; Sinskaya 1964).

The basic taxonomical category, however, is the species. For geobotanical investigations in wild plants the use of more detailed categories, i.e. infraspecific taxa, is not essential. In the early days researchers concentrated on the level of the genera; later the species level was elaborated. At present taxonomists of cultivated plants should focus on the infraspecific level.

The taxonomical classification of cultivated plants depends on the methods on which it is based, and the attention which was paid to a given species. In general the economic relevance of a species favors scientific interest.

The classification of wheats

As early as 1935 Vavilov stated that "a basic handicap of all genetic investigation in wheat, as well as in other plants, is the accidental choice of the material... and the neglect of the wide range of geographical variation."

For crops, which have a short history of domestication, the characterization of a cultivar can be as general as for the botanical species. Wheat has been the basic element of food for humans for 10,000 years, and is to be found nearly all over the world. The resulting range of variation of wheat, as evident from Table 4, is astonishing. The formation of new infraspecific varieties is a continuous process during cultivation of the species. The modern techniques used in plant breeding of today never led to formation of such varieties. The latest systematical overview for wheat was finished in 1979 (Table 4), and it differs from the system established by Flaksberger in 1935 (Table 5). In particular, the latest system was cleared of contradictions and inconsistencies. The first successful approach to such a classification of wheat was done by Flaksberger in 1915. The system proposed by Percival (1921) does not differ very much from the latter. The ideas about the infraspecific differentiation of the species *T. aestivum* were very much changed owing to the expeditions of Vavilov to Central Asia, Iran, Afghanistan and India.

Table 4. Taxa in the genus *Triticum* (according to Dorofeev *et al.* 1979).

Species	Subsp.	Convar.	Subconvar.	Var.	Forms	Ecological groups
T. aestivum	2	3	4	194	15	23
T. aethiopicum	3	5	-	203		
T. araraticum	2	-	-	13		
T. boeoticum	2	-	-	61		
T. carthlicum	-	-	-	18	3	
T. compactum	2	3	4	96	2	9
T. dicoccoides	-	3	-	25		
T. dicoccon	4	4	-	64	2	
T. durum	2	6	3	120	30	12
T. ispahanicum	-	-	-	2		
T. jakubzineri	-	-	-	1		
T. karamyschevii	-	-	-	2		
T. macha	-	2	2	14		
T. monococcum	-	-	-	14	6	7
T. petropavlovskyi	-	-	-	4		
T. polonicum	2	2	-	41	1	3
T. sinskajae	-	-	-	1		
T. spelta	2	2	-	55	-	2
T. sphaerococcum	-	-	-	17		
T. timopheevii	-	-	-	4		
T. turanicum	-	-	-	20	-	2
T. turgidum	-	2	-	71	-	5
T. urartu	-	-	-	6		
T. vavilovii	-	-	-	7		
T. zhukovskyi	-	-	-	1		
Total = 25	21	32	13	1054	59	63

Table 5. Taxa in the genus *Triticum* (according to Flaksberger 1935).

Species	Subsp.	Proles	Sub-proles	Groups	Greges	Var.	Forms
T. aestivum (T. vulgare)	2	15	5	5	25	128	
T. carthlicum						10	2
T. compactum	2	3	1	1	21	68	
T. dicoccoides	2	3				25	22
T. dicoccon	5	6	3		4	65	8
T. durum	2	21	10	11	35	131	15
T. macha				2		8	
T. monococcum		3			11	2	11
T. polonicum	2				9	24	
T. spelta		2			9	3	
T. sphaerococcum						6	
T. spontaneum	2					23	46
T. timopheevii						2	
T. turgidum		2	5			19	138
Total = 14	19	58	19	19	133	633	104

The enormous diversity of wheat in Southwest Asia caused Vavilov to revise the value of the investigated characters of wheat for systematics. He noted that the endemic wheats are characterized by complexes of traits, which themselves are connected with distinct areas.

The endemic forms of Pamir Mountains, for example, can be distinguished by eligulatum forms and forms with more or less inflated ears. The characters themselves are connected with each other. By studying variability in wheat, Vavilov determined the hierarchy of characters according to their taxonomic value.

In the species *T. aestivum* there is a complex of characters connected with difficult threshing and stiff ears. These traits are always accompanied by several others: rough stalks and ears, xerophytic type. Such wheat is typical of southwestern Asia [subsp. *hadropyrum* (Flaksb.) Tzvel.]. Types with easy threshing ability, on the other hand, are peculiar to Europe and areas of less continental climate of Asia (subsp. *indoeuropaeum* Vav.). These are the two main geographical groups of wheat, which can be distinguished. Vavilov and Flaksberger (1935) regarded them as subspecies, using different names for them.

The study of the variation led to a more detailed insight, and allowed complete description of the geographical-botanical structure by an ecogeographical system of classification. This system also uses the more detailed taxonomical unit 'varietas'. The necessity to use more detailed taxonomical units was stressed by Sinskaja (1966), Hawkes (1970), Skvortsov (1971) and others.

The results of such a classification for *T. aestivum* are shown in Box 1. The Asian subspecies (subsp. *hadropyrum*) contains three groups of different geographical origin.

After the analysis of the European subspecies (subsp. *aestivum*) as well as the Asian subspecies (subsp. *hadropyrum*) it became obvious that the awned varieties of *T. aestivum* mostly belong to the semi-rough-eared type of wheat.
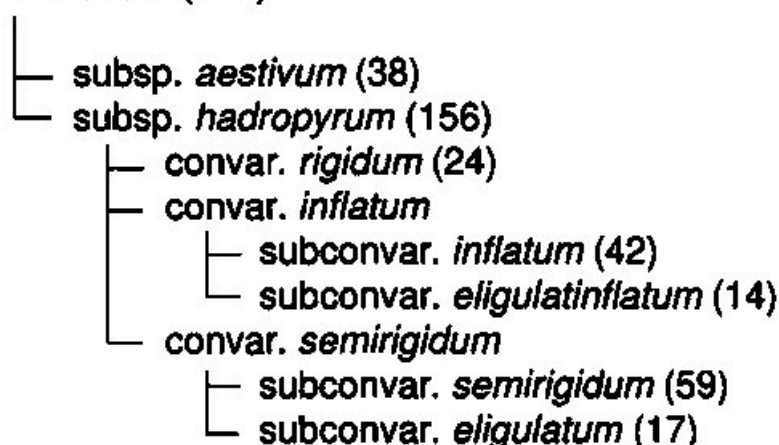
Box 1 shows that the Asian subspecies is of greater polymorphism. In particular, Middle Asia is a subarea of intense evolution of different types of *T. aestivum.* The subspecies *aestivum* is younger. Not consisting of so many ecogeographical groups, it is, nevertheless, characterized by very contrasting ecological groups. Length of the vegetative period, winter hardiness, resistance to diseases and other characters vary to a great extent. This subspecies covers a greater area, and stretches all over the European continent. The European subspecies has been affected by different types of ecological conditions, by different types of agriculture and by modern plant breeding.

Places with a long tradition of wheat cultivation, resulting in special ecogeographical types, could be singled out. At present these landraces are to a great extent used as basic material in plant breeding.

Triticum compactum, having much in common with bread wheat (*T. aestivum*)*,* was widely cultivated in the past and concurrently developed in environments similar to those of bread wheat; thus it repeats the polymorphism of bread wheat (Box 2).

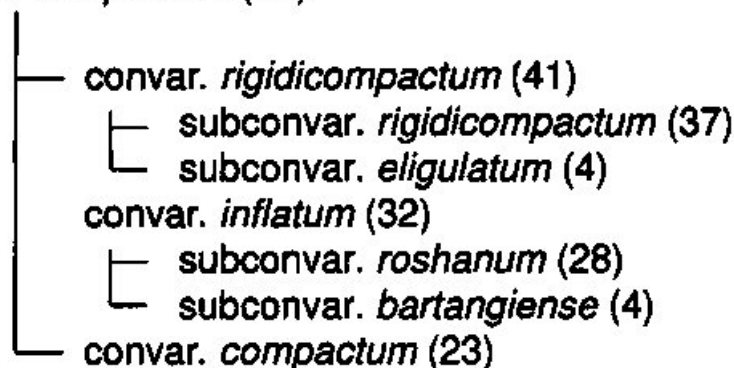**Box 1. Infraspecific classification of *Triticum aestivum* L.**

T. aestivum (194)[1]

- subsp. *aestivum* (38)
- subsp. *hadropyrum* (156)
  - convar. *rigidum* (24)
  - convar. *inflatum*
    - subconvar. *inflatum* (42)
    - subconvar. *eligulatinflatum* (14)
  - convar. *semirigidum*
    - subconvar. *semirigidum* (59)
    - subconvar. *eligulatum* (17)

[1] **Number of botanical varieties in parentheses.**

Box 2. Infraspecific classification of *Triticum compactum* Host

T. compactum (96)[1]

- convar. *rigidicompactum* (41)
  - subconvar. *rigidicompactum* (37)
  - subconvar. *eligulatum* (4)
- convar. *inflatum* (32)
  - subconvar. *roshanum* (28)
  - subconvar. *bartangiense* (4)
- convar. *compactum* (23)

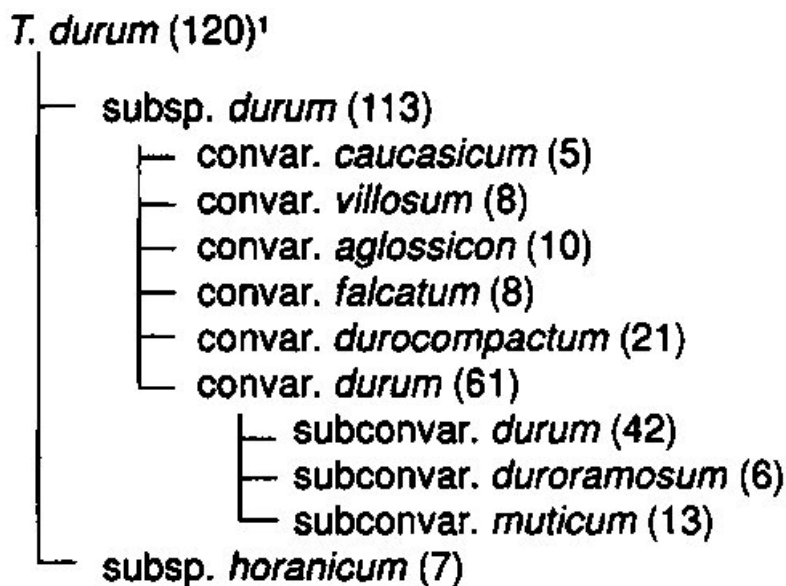[1] **Number of botanical varieties in parentheses.**

Reduction of the area of distribution of *T. compactum,* which took place in the remote past, and restriction of cultivation of this wheat mainly to mountainous zones led to elimination of sharply contrasting groups. No distinct isolation of subspecies is observed within this species. Flaksberger (1935) supposed that the process of differentiation in *T. compactum* had stopped in those distant historical times when cultivation

of this wheat started to be replaced by more productive bread wheat.

The system of infraspecific classification of *T. durum* is completely different. This wheat species is, after *T. aestivum*, the species with the widest range of geographic distribution (Box 3). Virtually different is the differentiation pattern of the second most important wheat species in terms of distribution, *T. durum* (Box 3). There is no complicated branching structure like the one observed in bread or compact wheats. The area of durum wheat stretches along the Old Mediterranean from west to east.
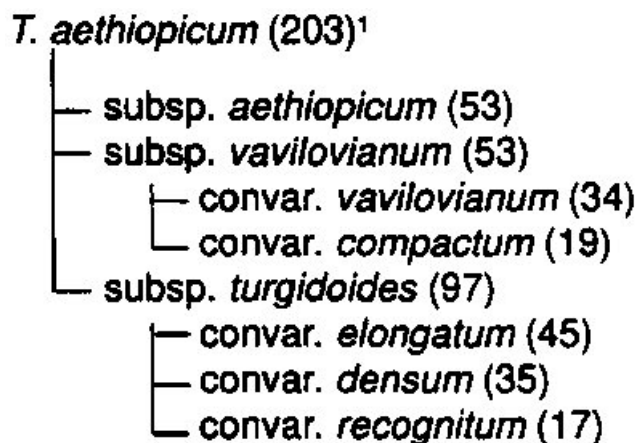
Durum wheat has no distinctly isolated ecological groups. The most definite are morphological differences in khoranka wheats (subsp. *horanicum*), which are characterized by a certain genetic isolation (in crosses with proper durum wheat, anomalies and sterility of the progeny may be observed). This feature preconditioned their separation into a subspecies of *T. durum,* known as subsp. *horanicum* Vav. Basically durum wheat is united by the presence of numerous common traits having similar manifestations along the whole stretched area of its distribution. However, separate distinct features and their sets have a local character, i.e. they are geographically attributed: isolation of groups regulated by selection took place long ago. To describe such type of infraspecific structural subunits the taxon of 'convarietas' (group of varieties) was used. The intraspecific classification of other wheat species (*T. aethiopicum, T. turgidum* and *T. polonicum*) is less complicated and the number of botanical varieties is limited (Boxes 4 and 5). Owing to the indiscrete continuity of evolutionary processes there are almost always transitional forms (most easily preserved by humans in the case of self-pollinators).

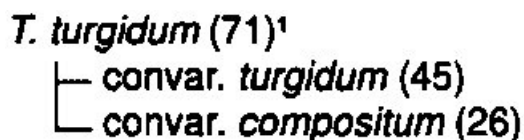**Box 3. Infraspecific classification of *Triticum durum* Desf.**

T. durum (120)[1]
- subsp. *durum* (113)
  - convar. *caucasicum* (5)
  - convar. *villosum* (8)
  - convar. *aglossicon* (10)
  - convar. *falcatum* (8)
  - convar. *durocompactum* (21)
  - convar. *durum* (61)
    - subconvar. *durum* (42)
    - subconvar. *duroramosum* (6)
    - subconvar. *muticum* (13)
- subsp. *horanicum* (7)

[1] Number of botanical varieties in parentheses.

Box 4. Infraspecific classification of *Triticum aethiopicum* Jakubz.

T. aethiopicum (203)[1]
- subsp. *aethiopicum* (53)
- subsp. *vavilovianum* (53)
  - convar. *vavilovianum* (34)
  - convar. *compactum* (19)
- subsp. *turgidoides* (97)
  - convar. *elongatum* (45)
  - convar. *densum* (35)
  - convar. *recognitum* (17)

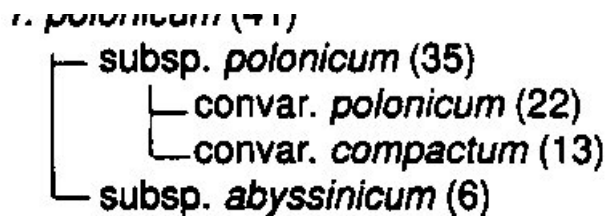[1] Number of botanical varieties in parentheses.

Box 5. Infraspecific classification of *Triticum turgidum* L. and *Triticum polonicum* L.

T. turgidum (71)[1]
- convar. *turgidum* (45)
- convar. *compositum* (26)

T. polonicum (41)

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T. polonicum (41)
├── subsp. polonicum (35)
│         └── convar. polonicum (22)
│         └── convar. compactum (13)
└── subsp. abyssinicum (6)
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¹ Number of botanical varieties in parentheses.

Conclusions

For the identification and preservation of the global crop genetic diversity it is necessary to:

- develop infraspecific classifications for all crops with a relevant variation

- make inventories of genebank collections according to the most detailed and reliable classification available

- work out a unified system of classification units with due respect to the specific features of cultivated plants (at the present stage it would be sufficient to use the system presented by the International Code of Botanical Nomenclature)

- make the ecogeographic zoning of the earth more precise by defining boundaries of regions, subregions, areas of influence, etc., and accomplish detailed inventories of cultivated plant diversity in these territories.

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Archaeobotanical Evidence for the Beginnings of Agriculture in Southwest Asia - G. Willcox

Introduction

Over the past ten years much new evidence has to come to light which has enabled us to explain in more detail the transition from plant-gathering to plant production in Southwest Asia. It is now clear that this important change, which led ultimately to a significant increase in population, urbanism in Mesopotamia and Egypt, the civilizations of Greece and Rome and eventually industrialization, occurred gradually over a long period in a geographically wide area. Over 30 sites have provided a corpus of botanical evidence for the plants used during this period. These plant remains themselves have provided several hundred radiocarbon dates.

Archaeobotanical evidence indicates that the process of domestication may have been slow (Willcox 1995), and finds indicate that domestic and wild cereals occurred as mixtures on several early Neolithic sites over a period of at least a millennium (Table 1). Archaeobotanical finds and field studies show clearly that late Epipalaeolithic and early Neolithic distributions of wild cereals were much more extensive (Hillman 1996) and that the cereals collected differed on the various sites according to variations in local conditions which favored certain cereals (barley on poor dry soils, for example). These differences can be seen prior to and just after cultivation began. But once cultivation became systematic, favorable soils would have been chosen as would preferred crops. For example, emmer became more widespread at the expense of einkorn. Sites geographically separated with long sequences appear to show gradual evolution toward domestication, which may have occurred independently.

Methods

Archaeobotanical samples have been obtained from 35 sites (see Fig. 1) in southwestern Asia from the crucial period 20,000 to 8500 BP (non-calibrated). The quantity and quality of the archaeobotanical information vary considerably between sites. Because biological decomposition is rapid in the aerobic archaeological sediments of this area, archaeobotanists rely on plant materials which have been rendered stable through charring in hearths or other fires. These remains are recovered by flotation and sieving. Under the best circumstances large-scale flotation has obtained thousands of charred seeds, fruits and fragments of charcoal within the chronological framework of a site. At worst no sampling was carried out or only a few chance finds were collected. This makes comparisons between certain sites difficult.

Concerning the archaeobotanical criteria for morphological domestication and cultivation, not all archaeobotanists agree on the best criteria. The solid rachides in barley and naked wheats are clear indicators for archaeobotanists. However, the more primitive hulled wheats such as einkorn and emmer are more problematical. For the archaeobotanist the distinction between domestic and wild hulled wheats is based on the disarticulation scar left by the abscission layer. The break occurs in the same place on the rachis, and on domestic modern material it is rough or torn and on wild material it is smooth. However, with ancient carbonized remains the surface is very often too poorly preserved to allow this distinction.

Grain size is another criterion used, because domestic grains are generally more plump (van Zeist and Roller 1994). Plump barley grains, unknown in the wild, occur with fragile rachis fragments on a number of sites, e.g. at D'jade, Mureybit and Jerf el Ahmar. These are not considered to be evidence of domestication. However there is some reason to reconsider these finds in the light of modern semi-solid rachis barley which occurs in Syria. The author has collected specimens of semi-solid rachis, two-row 'black' barley near Bosra in southern Syria. The disarticulation scar is similar to that of wild barley, and the rachis fragments would be difficult to distinguish from wild types in carbonized material. This morphological type could explain why domestic-type grains occur with apparent wild-type rachis fragments.

As for evidence for cultivation, one might expect digging tools to provide the answer. However, for the moment this is not the case and it is possible that these tools were wooden and have not survived. Archaeobotanical research has concentrated on the presence of weed assemblages (Hillman *et al.* 1989; Colledge 1994). At present there are no solid results but sites with wild cereals are sometimes accompanied by an assemblage which resembles that of a weed flora. The most common taxa in these assemblages include the following: *Adonis, Aegilops, Astragalus, Avena, Bromus, Bupleurum, Camelina, Centaurea, Centranthus, Coronilla, Fumaria, Galium, Glaucium, Hordeum, Lathyrus, Lithospernum, Lolium, Malva, Papaver, Polygonum, Reseda, Silene, Valerianella* and *Vicia*. It is difficult to be sure that these taxa really represent a weed assemblage because these plants make up part of the original steppe flora, and identification at the species level is rarely possible. On the other hand, what one might expect is an increase in the frequency of these taxa at the expense of other steppe plants which were not preadapted to become part of the weed flora.

Archaeobotanical results

A summary of archaeobotanical results is given in Table 1. Several late Palaeolithic hunter-gatherer cultures have been recognized in Southwest Asia for the period 20,000-12,000 BP. Archaeobotanical evidence from this period is sparse because hunter-gatherers are mobile and thus archaeological deposits are superficial, which does not favor survival of carbonized plant remains. The early part of this period coincides with the glacial maximum in Europe. High-altitude pollen sites in Turkey and Iran indicate steppe conditions. Further south near the Mediterranean, conditions were more favorable. The earliest evidence for grain exploitation comes from widely separated sites: Ohalo II (Kislev *et al.* 1992) near the sea of Galilee, dated to 19,000 BP, is the earliest find (wild pulses, emmer and barley) and corresponds to the glacial maximum. Wild grasses were recovered from Wadi el-Jilat 6 (a little later in date) in the Jordan steppe. At Franchthi cave in Greece, dated to 12,500 BP, wild barley and pulses were found (Hansen 1991). These sites are all that has been found of what was probably a widespread phenomenon. It is probable that these hunter-gatherers roamed widely in the region. Wild cereals and pulses would have become more and more abundant during the late glacial climatic amelioration. Groundstone tools, originally used perhaps for ochre, may have been adapted for cereal processing.

Table 1. Presence of the major cereals, pulses and tree species from sites in the eastern Mediterranean (adapted from Nesbitt and Samuel 1996). There is considerable chronological overlap between sites, particularly for the later periods. Note that lentils are very frequent; domestication appears over a wide area during the last half of the 10th millennium BP. Oak is also well represented.

Site	Date BP non-cal.	Einkorn w†	emmer w†	barley w†	einkorn d†	emmer d†	naked wheat d†	barley 2r d†	barley 6r d†	*Aegilops* w†	lentil ?†	pea ?†	bitter vetch ?†	oak w†	almond w†	*Pistacia* w†	flax ?†	Reference
Ohalo II	19,000	-	O‡	O	-	-	-	-	-	-	O	-	-	A‡	O	O	-	Kislev *et al.* 1992
Franchthi	12,400-9000	-	-	O	-	-	-	-	-	-	O	O	O	-	O	O	-	Hansen 1991
Hayonim	12,300-11,900	-	-	O	-	-	-	-	-	-	O	-	O	-	-	-	-	Hopf and Bar Yosef 1987
Wadi Hammeh 27	12,200-11,900	-	-	O	-	-	-	-	-	-	O	-	-	W‡	-	O	-	Willcox 1991 a; Colledge 1994
Abu Hureyra 1	11,000-10,000	O	-	O	-	-	-	-	-	-	O	-	O	W	W	O	-	Hillman *et al.* 1989
Hallan Çemi	10,600-9900	-	-	-	-	-	-	-	-	-	O	-	O	-	O	O	-	Rosenberg *et al.* 1995
Mureybit I-III	10,200-9500	O	-	O	-	-	-	-	-	-	O	-	-	W	-	O	-	van Zeist & Bakker-Heeres 1984
Qermez	10,100-	-	-	O	-	-	-	-	-	-	O	-	O	-	-	O	-	Nesbitt

Site	Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Reference
Dere	9700																	1995
Netiv Hagdud	10,000-9400	-	-	O	-	-	-	-	-	O	-	-	-	-	-	-	-	Bar-Yosef *et al.* 1991
Jerf el Ahmar	9800-9700	O	-	O	-	-	-	-	-	O	O	O	O	W	O	O	-	Willcox 1996
M'lefaat	9800-9600	?‡	-	O	-	-	-	-	-	O	?	-	O	-	-	O	-	Nesbitt 1995
Tell Aswad Ia	9700-9600	-	-	O	-	?	-	?	-	-	O	O	O	-	O	O	-	van Zeist & Bakker-Heeres 1984
D'jade	9600-9000	O	-	O	-	?	-	-	-	-	O	O	O	W	O	O	-	Willcox 1996
Cayönü mr	9500-9200	?	?	-	-	-	-	-	-	O	-	-	-	W	O	O	-	van Zeist and de Roller 1994
Jericho PPNA	9500-9000	-	-	?	?	?	-	?	-	-	O	-	-	-	O	O	-	Hopf 1983
Mureybit IV	9400-8500	O	-	O	-	-	-	-	-	-	O	-	-	W	-	O	-	van Zeist & Bakker-Heeres 1984
Cafer Höyük XIII-X	9400-9000	O	O	-	O	O	-	-	-	-	O	O	O	W	O	O	-	Willcox 1991c; de Moulins 1993
Tell Aswad Ib	9300-8800	-	-	O	-	O	-	?	-	O	O	-	-	-	-	O	-	van Zeist & Bakker-Heeres 1984
Cayönü gp bp ch	9200-8500	O	O	?	O	O	-	?	-	O	O	O	O	W	O	O	O	van Zeist and de Roller 1994
Nevali Cori	9200	-	-	?	O	-	-	-	-	O	O	O	O	-	O	O	-	Pasternak 1995
Ain Ghazal	9000-8500	-	-	-	-	O	-	O	-	-	O	O	-	W	-	O	O	Rollefson *et al.* 1985
Jericho PPNB	9000-8500	-	-	O	O	O	-	O	-	O	O	-	-	-	-	-	O	Hopf 1983
Cafer Höyük IX-VI	9000-8400	O	-	-	-	O	-	-	-	O	-	-	-	W	W	O	-	de Moulins 1993
Nahal Hemar	9000-8200	-	-	-	-	O	-	O	-	-	O	-	-	A	O	O	-	Kislev 1988
Beidha	8900-8700	-	-	-	O	O	-	?	-	O	-	-	-	-	-	O	-	Helbaek 1966
Ganj Dareh	8900-8200	-	-	O	-	-	-	O	-	O	-	-	-	-	-	O	-	van Zeist *et al.* 1986
Ali Kosh BM	8800-8000	O	-	O	O	O	-	O	O	-	-	-	-	A	-	O	-	Helbaek 1969
Jilat 7	8800-8400	O	-	O	O	O	-	-	O	-	-	-	O	-	-	O	-	Colledge 1994
Asikli	8800-8400	O	-	-	?	O	O	O	O	-	O	O	O	-	O	O	-	van Zeist and de Roller 1995
Abu Hureyra PPNB	8800-8000	O	-	O	O	O	O	O	-	O	O	-	-	W	W	O	-	de Moulins 1993
Tell Aswad II	8700-8400	O	-	O	O	O	O	O	-	O	O	-	-	-	-	O	O	van Zeist & Bakker-Heeres 1984
Ghoraifé I	8700-8100	-	-	O	-	O	O	O	-	O	O	-	-	-	-	O	O	van Zeist & Bakker-Heeres 1984
Abdul Hosein	8700-7500	-	-	-	-	O	-	O	-	O	-	-	-	-	W	O	-	Hubbard 1990; Willcox 1990
Halula	8700	?	O	O	-	O	O	O	-	O	O	O	O	W	-	O	O	Willcox 1996
Magzalia	8600-	-	-	O	-	O	O	O	-	O	O	-	-	-	-	-	-	Willcox,

Site	Date																	Reference
	7800																	unpublished
Gritille	8500-7700	-	-	-	-	O	-	O	-	-	O	-	O	-	-	-	-	Voigt 1984
Can Hassan III	8500-7600	O	O	-	O	O	O	O	-	-	O	-	O	W	O	O	-	French et al. 1972
Jarmo	8500	O	O	O	O	O	-	O	-	-	O	-	-	W	-	O	-	Braidwood and Braidwood 1983

† **W** = wild, **d** = domestic, **?** = wild and/or domestic.

‡ O = present, ? = identification based on small number of poorly preserved finds, W = identification based on wood, A = acorn.

Fig. 1. Map showing the distribution of sites mentioned in the text.

The site of Franchthi cave in Greece is not included in the map for reasons of scale.

Food grains have the immense advantage that they can be stored. The wild grasses become ripe in late spring and promptly fall to the ground. They need to be harvested just before maturity. Given the dry climatic conditions, grains can be conserved or stored relatively easily. This facility for storage was one of the main advantages of seed-gathering which led to a more secure subsistence base and prepared the way for a sedentary way of life.

Increasingly favorable climatic conditions resulted in a rich environment for Early Natufian inhabitants of the western Mediterranean (12,000-11,000 BP). The climate appears to have been more favorable than at present or at any time since the Natufian. Archaeobotanical evidence indicates that the Syrian and Jordanian steppes had a much richer vegetation. This is indicated by the presence of forest steppe species, for example *Pistacia* and *Amygdalus.* Cultural factors such as an increased reliance on stored grain (although there is little archaeological evidence for this) permitted a sedentary existence, which is shown by the appearance of the first village sites consisting of what appear to be the first permanent dwellings. Sites such as Mureybit and Abu Hureyra on the Euphrates in Syria, Hayonim in Israel, Wadi Hammeh in Jordan, and a little later Qermez Dere, Nemrik 9 and M'lefaat in northern Iraq have round architecture, large hearths and groundstone equipment. On these sites the archaeobotanical evidence indicates that wild cereals were exploited together with a number of edible fruits and pulses (lentils occur on all sites). Charcoal and fruit remains indicate that these sites were situated within the forest/steppe with *Pistacia* and almond; in favorable conditions, deciduous oak was present. Archaeobotanical evidence clearly indicates that this vegetation penetrated further east into what is now arid steppe. This habitat provided wild cereals, pulses and an abundance of game. At sites where plant remains were not recovered, indirect evidence for the use of grasses comes from glossed flint tools indicating the harvesting of plants with high silica content at the Epipalaeolithic sites of Nahal Oren, Hatoula and Kebara in Israel and Beidha in Jordan (Anderson 1994, and pers. comm.).

It is clear that morphologically wild progenitors of Old World cereals and legumes were exploited for several millennia, before the appearance of their domestic counterparts. The geographical extent is impressive, stretching from northern Iraq to the southern Levant, Anatolia and even southeast Europe. During this period regional differences can be seen between Epipalaeolithic sites. Einkorn is dominant at Mureybit and Abu Hureyra, barley and some emmer are present at Ohalo II. Rye is also present at a number of these sites (Hillman *et al.* 1993), which indicates cooler climatic conditions.

During the Late Natufian there is wide evidence for climatic deterioration from about 11,000, usually referred to as the Younger Dryas (Baruch and Bottema 1991), which appears to have adversely affected settlements in the more arid zones of the Jordanian and Syrian steppe and the Negev highlands. With few exceptions, these sites were abandoned, and only sites situated near permanent water continued to be occupied into the next period.

During the following period, the Pre-Pottery Neolithic A (PPNA, 10,000-9600 BP), the climate became more favorable again. Charcoal evidence indicates that the Syrian steppe was at least partly wooded. But the sites continue to occur near reliable water sources. The architecture of small round houses is more substantial. Key sites are Jericho, Cayönü, Aswad, Mureybit, Jerf al Ahmar and Netiv Hagdud (Bar-Yosef *et al.* 1991). No unequivocal morphological evidence for domestication is forthcoming. For the very earliest levels at Aswad IA and Jericho, remains are numerically too meagre to be certain of domestication, but what is clear for this period is that the plant/crop assemblages vary remarkably between sites. Emmer is dominant at Aswad (van Zeist and Bakker-Heeres 1982), einkorn at Mureybit, barley at Jerf al Ahmar in northern Syria (Table 2). This suggests that the inhabitants of these sites were still gathering local cereals but this does not exclude small-scale cultivation as described by Harris (1996), using locally available wild cereals as seed stock. Lentils are common on most sites, even in the most arid zones. The controversial plump domestic-type barley grains (see Fig. 2) associated with wild-type rachis fragments occur during this period.

Sites such as Jericho, Cayönü, Mureybit, Abu Hureyra and Aswad which were established during this period or earlier show no clear-cut domestication in the lowest levels, but morphological domestication does appear at higher levels. These sites appear to have been occupied (probably continuously) over a very long period, more than a millennium. This would have led to degradation of the local vegetation within the catchment area of the site. Thus resource depletion could have been a contributing factor for the adoption of agriculture.

During the next chronological period (Early PPNB, 9600-9000 BP), architecture becomes rectangular and the transition is seen on a number of sites. Emmer domestication has been reported for sites such as Cafer Höyük and Cayönü in eastern Anatolia and for Aswad near Damascus (however, some researchers prefer to rely on the solid rachis in barley and the naked wheats as sure evidence for domestication, especially when sample size is small). At Aswad, between 9730 and 8560 BP (PPNA and Early PPNB), 26% of the barley rachis fragments are solid domestic types, but it is not clear whether they occur in the earliest levels. At D'jade (Willcox 1996) preliminary studies indicate that the cereals are not yet domesticated, but indirect evidence of weed associations strongly suggests the presence of cultivation, and similar assemblages are seen at Aswad, Cayönü and Cafer Höyük.

The Middle PPNB (9200-8600 BP) sites are more extensive, more frequent and cover a wider geographical area with expansion of agricultural communities into central Anatolia (Asikli Höyük) and Cyprus (Shillourokambos). Crop evolution and morphological domestication are clearly shown by the appearance of a solid rachis in barley and naked wheat, for example at Aswad West phase II (van Zeist and Bakker-Heeres 1982) and at Asikli (van Zeist and Roller 1995).

In the Euphrates Valley there is no evidence for *in situ* domestication unless we consider the plump barley grains from PPNA sites as domestic. Instead domesticates were introduced. Emmer absent in the area during earlier periods appears to have been introduced from

elsewhere at Abu Hureyra and Halula together with a naked wheat (Willcox 1995, 1996). Flax was introduced at Halula.

At many sites during this period wild types remain at significant frequencies. We can see this at Cayönü, Cafer Höyük (wild wheats), Aswad, Ganj Dareh (wild barley), Halula and Azraq (wild wheats and barley) (Colledge 1994). These mixed finds can be interpreted in three ways: (1) as evidence of the exploitation of wild stands, (2) as unwanted weeds, and (3) as an integral part of the crop consisting of a mixture of wild and domestic cereals. The relatively high proportion of wild types and the lack of pure finds of domesticates suggests that the wild plants may have been considered as a useful part of the crop, as opposed to unwanted weeds. This suggests cultivation of wild and domestic types together but does not exclude gathering from wild stands in a kind of mixed economy. Even during later periods (Late PPNB, 8600-8000 BP), for example at Ramad between 8210 and 7880 BP, domestic barley rachis fragments are only at 52%. A similar situation was noted at Magzalia. However at other contemporary sites such as Bouqras (van Zeist and van Waterbolk 1985) and Ras Shamra (phase Vc) wild types are rare or absent. These sites also contain naked wheat. During the Late PPNB, einkorn becomes a minor component and could be interpreted as a weed for most of the Near East. It reappears as a major component later at Jeitun in Central Asia (Harris *et al.* 1992) and at many sites in Europe.

Table 2. Comparison of percentages of cereals at four PPNA sites. The differences indicate that the inhabitants were still using local cereals rather than introduced crops which start to appear in Middle PPNB.

	Jerf el Ahmar	Mureybit	Aswad Ia	Netiv Hagdud
Einkorn	15.8	96	0	0
Emmer	0	0	89.5	present
Barley	84.2	4	10.5	dominant

Taking the data from the PPNA and the PPNB together, there is evidence for independent *in situ* cereal domestication at different sites. As we have seen, even sites in the same area had different cereal assemblages during the PPNA such as Jerf el Ahmar and Mureybit. The evidence from sites with long sequences such as Aswad, Mureybit, Cafer Höyük and Cayönü points to separate and distinct evolutionary trends. At Cayönü wild-type emmer grains are progressively replaced by domestic types (van Zeist and Roller 1995) and barley remains wild, whereas at Aswad and nearby Ghoraifé, as already mentioned, wild-type barley rachis internodes are replaced progressively by solid-type domestic rachis fragments (van Zeist and Bakker-Heeres 1982). The period of time necessary to recognize these changes appears to be about a millennium, that is to say between the early 10th and early 9th millennia. Other sites such as Mureybit show no evolutionary trends; however, taxa which are interpreted as weed assemblages at other sites are present. For example at Cayönü similar taxa are considered by van Zeist to be potential field weeds; these taxa also occur at other PPNA sites, suggesting predomestic agriculture.

Experimental results indicate that particular agricultural conditions are necessary for domestication to occur. As Hillman and Davies (1990) point out, both seed corn from the wild and that originating from fallen spikelets during the harvest must be kept apart, and in reality this is not easy. This could explain why significant mixtures occur over a period of at least a millennium and would appear to indicate that selective pressures stayed relatively low. If this interpretation is correct, then it follows that cultivation without domestication would have occurred for some considerable time prior to the appearance of the solid rachis. If this is indeed the case, then archaeobotanists need to look for indirect indicators. Hillman examined the possibility of identifying a weed assemblage from Epipalaeolithic Abu Hureyra (Hillman *et al.* 1989). His results were negative. Preliminary results from a later site, D'jade, on the Euphrates (Willcox 1996), look more promising.

Conclusions

Archaeobotanical evidence indicates that wild cereals were exploited in the Near East for several millennia before the appearance of domestic types. Specialized gathering and especially storage of cereals and pulses would have provided a secure subsistence base, making possible a sedentary existence. In the northern Levant it is not clear whether early 10th millennium cereals were domesticated. During the second half of the 10th millennium there is evidence of emmer domestication. However, a millennium after the appearance of domestication, wild types still persisted at frequencies which suggest they were part of the crop rather than unwanted weeds. Archaeobotanical and experimental evidence indicate that cereal cultivation of progenitors does not necessarily lead to rapid domestication and that gathering from the wild continued to be practised long after domestication. However, a number of scholars insist that domestication was a rapid process, suggesting that after the appearance of a given mutation the establishment of mutant lines could take place in a few years (McCorriston and Hole 1991; Zohary 1996). They therefore see the appearance of domestication as simultaneous with the beginnings of cultivation.

The area occupied by pre-Neolithic cereal gatherers is vast, which suggests the possibility that domestication could have occurred independently in different localities. Indeed genetic evidence points to at least two different origins for barley and according to Zohary, emmer and the pulses were taken into cultivation perhaps "once or at most only very few times" (Zohary 1996). However, still other varieties may have been taken into cultivation but subsequently died out or do not show up because of genetic modifications which have occurred over the last 10,000 years. As we have seen, the archaeobotanical evidence also indicates the possibility that the domestication process occurred independently at different sites.

The point at which people started to cultivate remains elusive, but small-scale or intermittent cultivation of pulses and perhaps cereals may have occurred over a long period (PPNA and earlier) without leading to domestication, as suggested by Kislev (1992). Not until large-scale cereal cultivation in the Middle PPNB do we see the appearance of domestic barley and naked wheat and the spread of emmer.

It would appear that the transition to a production economy was gradual, as there is no evidence for an abrupt change. During the period of transition there was little need for innovation in material culture. The tools for processing of gathered and cultivated cereals remain essentially the same. Storage, and storage structures, could be the same for both economic systems. During the late Epipalaeolithic one might consider the possibility that natural wild stands were to some extent managed to avoid overexploitation. Then occasional sowing was adopted. Inadvertent or accidental sowing around crop-processing areas during the collecting stage is inevitable and could hardly have been totally ignored. Later it would have become clear that sowing would be enhanced if the soil was worked, and it is possible that suitable tools already existed for other activities such as collecting earth for building or digging up roots and tubers.

Environmental change could have resulted from climatic change or human activities in the catchment area. This could have been a contributing factor in the transition from a subsistence system to a production economy in the Near East. The best-documented climatic change is the return of cooler, drier conditions (Younger Dryas) between 11,000 and 10,000 BP (Moore and Hillman 1992). Given the steep gradient in isohyets between the mediterranean vegetation zone and the interior steppe zone, even a small climatic change in the marginal areas would have had a profound effect. This also means that populations could migrate in order to compensate for shifts in climate. Both major (Younger Dryas) and minor climatic episodes would have provided an impetus influencing communities to adapt in different ways. However, the evolution toward and the adaptation to a production economy with resulting domestication required certain preconditions. In other words it

required a combination of complex circumstances leading to an evolutionary path which resulted in an economy dependent on cereal cultivation. On the one hand the plants already used by humans would have to have the right biological attributes (see Zohary 1996) and on the other, humans had to have prerequisite behavioral attributes. They would have to be sedentary gatherers of wild progenitors with a minimum village size and a storage system. A certain social organization could also have been a contributing factor. As pointed out by Cauvin (1994), humans would have to be culturally ready. Once all these conditions were fulfilled, small-scale farming could start and this would perhaps in certain circumstances develop into a full-scale farming economy (symbiosis). This would provide a subsistence system where production was guaranteed to supply demand (and/or surplus) in an expanding economy, ultimately leading to an irreversible process. We are not in a position to say whether cultural change played a more important role than environmental change. To assume that a single factor such as climatic change or a cultural attribute could have led to the adoption of plant husbandry is too simplistic.

Fig. 2. Carbonized plant remains of *Triticum/Secale* grains; 1 and 2 (Jerf al Amhar) and 3 (D'jade). Plump-type barley grains which are not known in the wild but occur on PPNA sites associated with wild-type rachis fragments: 4 (Jerf al Ahmar), 5 and 6 (D'jade). This last grain is similar to two-row hulled domesticated barley but is associated with wild-type rachis fragments.
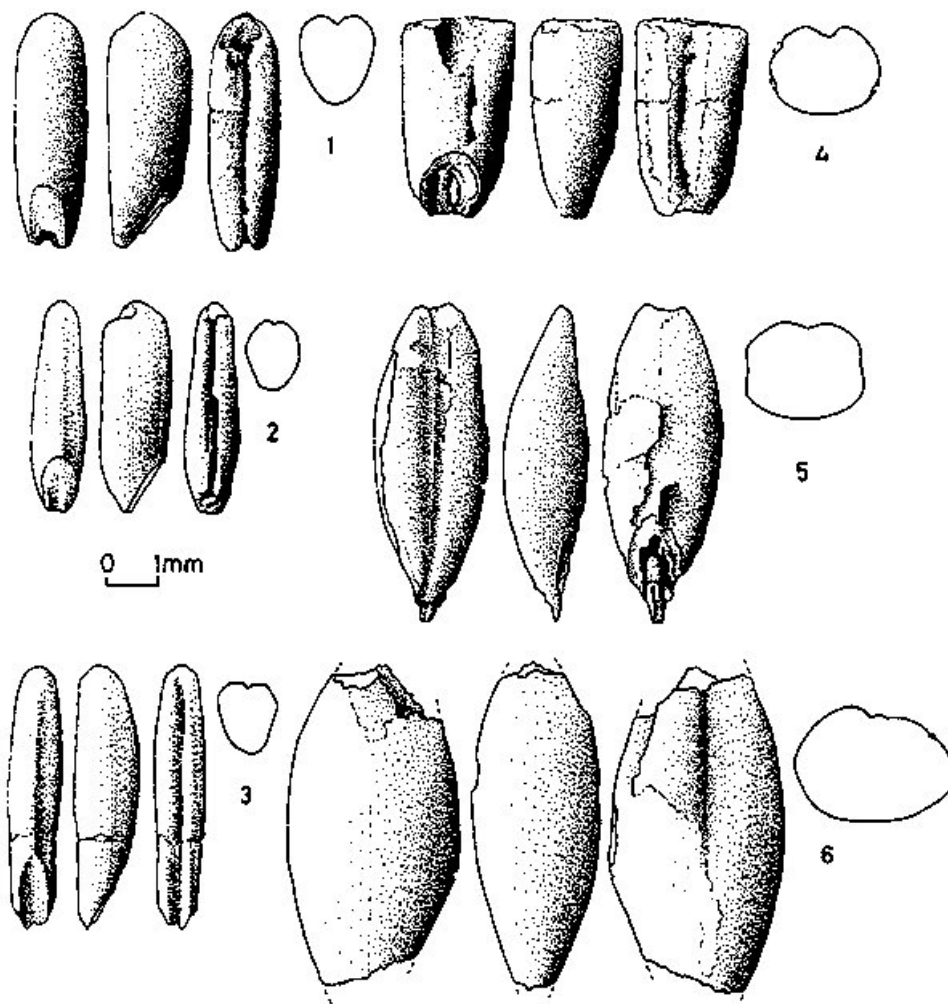
One might speculate that the cultivation of pulses and cereals during the 11th and 10th millennia could have been an occasional option, but not necessarily systematically adopted. If occasional domesticates arose they may not have survived in the long term. Climatic change in some areas may have favored cultivation as opposed to gathering as wild resources became depleted. Ultimately social organization developed to a point where farming became more and more organized, leading to high selective pressures for domestic types. Archaeological evidence during the Middle PPNB indicates the simultaneous emergence of rectilinear architecture, considerable increase in village size, the consistent appearance of domesticated cereals and the domestication of sheep and goats. Could these changes be correlated with a more developed and organized sociocultural system which became increasingly reliant on a highly managed agricultural system? This could have coincided with the adoption of rectangular field systems. Ultimately the process led to irreversible domestication combined with a steep rise in population. It appears that these changes were gradual and occurred more or less simultaneously over a wide area, that is to say the Euphrates Valley, Eastern Anatolia, the southern Levant and the Zagros foothills. Differences in material culture over the area as a whole are slight and contact across the region between geographically widely separated populations has been shown to occur from finds of marine shells and obsidian, which were traded across vast distances. If the area as a whole went through the pre-domestic cultivation stage, then it is highly probable that domestication of the so-called founder crops occurred independently in different areas. However at some sites, for example at Mureybit, only wild cereals were exploited during the Middle PPNB, while at the majority of sites, for this period, domestic cereals were predominant.

Acknowledgments

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Syrian Origins of Safflower Production: New Discoveries in the Agrarian Prehistory of the Habur Basin - J. McCorriston

Introduction

Half a century has passed since Vavilov's and Braidwood's pioneering research into the origins of agriculture in the Near East, and these years have seen tremendous progress in genetic and archaeological research into the first experiments with domesticating plants and the earliest agricultural societies. Archaeological research has established the identities of the first Neolithic farmers who settled and farmed domesticated plants without ceramics or domesticated animals. Excavations at early Neolithic sites have documented the Southwest Asian agricultural package largely predicted by Vavilov, i.e. wheat, barley, lentil, chickpea, pea, vetch and flax. With our hindsight emphasis on the tremendous success of agricultural lifestyles, it has been relatively easy for archaeologists and botanists alike to ignore or gloss over one of the salient characteristics of the Neolithic: these crops were independently domesticated and combined later into an agricultural package.

Much emphasis has been on the earliest Neolithic and the first transition to farming lifestyles, yet the process of domestication and the development of new agricultural technologies and farming strategies continued throughout Near Eastern prehistory, just as it continues today. And, as at present, every new technology and introduction into the crop repertoire had potentially enormous social consequences.

This paper discusses current research into the development of agriculture after its origins, focusing on the northern Syrian Jezireh. Introductions of new farming techniques and new crops played important roles in the ways people reorganized themselves to exploit land and vegetation in an expanding framework of interregional connections and exchange. Within this developing agricultural system and over many millennia, people's use of plants shifted frequently. By the 3rd millennium BC, people began manipulating wild *Carthamus* plants in patterns that point to its first exploitation as a dye and field hedge long before its seeds increased in size or shell thickness thinned for production of safflower oil.

Northern Mesopotamia after the Neolithic Revolution

Northern Mesopotamia was unquestionably a critical region for agricultural development and change after the first domestications of cereals and pulses in the Levantine arc of the Fertile Crescent. Herders' and farmers' lifestyles may have accommodated each other early in northern Mesopotamia, intermediate between Mediterranean lands (to which many new plant domesticates were adapted) and the Zagros or Taurus piedmonts where caprines were most probably domesticated (Hole 1987). The earliest northern Mesopotamian settlements such as Qermez Dere, M'lefaat and Nemrik 9 show little sign of such accommodation (Kozlowski 1989; Nesbitt and Watkins 1995) but archaeologists have noted the appearance of an integrated plant and animal husbandry at later sites such as Bouqras and Magzalia (Akkermans *et al.* 1983; van Zeist and van Rooijen 1985; Cauvin 1994). That the early incorporation of farming and herding economies was of profound importance in the development of agriculture has been widely recognized, but only more recently has attention shifted to the significance of other pioneering and variable strategies for food production after the Neolithic revolution (Zeder 1994).

Fig. 1. Map of upper and middle Habur drainage, Syria.

In northern Mesopotamia, a transect of environmental zones across the drainage of the Habur River (a Euphrates tributary) offers a rich field laboratory in which to examine agricultural development in different environmental settings (Fig. 1). The earliest farming settlements of this region appear in the 6th millennium BC in the north (Nishiaki 1992), where loam soils and rainfall in the range of 350-500 mm/year ensure crop production. South of Hassakeh precipitation declines and at current levels (250 mm/year) and high interannual variability, farming is risky. In wet years, a barley crop is possible on the gypseous soils of the steppe, but dependable farming today clings to the relatively rich river alluvium within range of irrigation pumps.

The first apparent farmers in this middle Habur region (between Hassakeh and Tell Ajaja) settled along the river in the 5th millennium BC (Hole and Johnson 1986-1987; McCorriston 1992). Only one site, Umm Qseir, still exists from this Halaf period. Pioneering farming settlements often are widely spaced (Stone 1997); furthermore, subsequent river shifts and human activities could have obliterated or obscured other early sites (e.g. Wilkinson and Tucker 1995). Settlement is also evident along the Habur River during the 4th millennium BC, but throughout early prehistory, the steppe apparently attracted human settlement only near springs and other permanent water sources.

The most distinctive settlement pattern in the middle Habur region is a spate of new settlements, some on virgin soil, evident from the beginning of the 3rd millennium BC. Settlements appear both along the river and in the steppe (van Liere and Lauffray 1954-1955; Röllig and Kühne 1977-1978; Monchambert 1984; Hole 1997). As recent rescue excavations have proceeded along the Habur River, excavators have speculated about the causes for an apparent settlement explosion in the 3rd millennium BC. Did inhabitants use the landscape differently? Were they taking advantage of better climate (Hole 1997), did the growing cities to the north or south forge widespread economic ties for their own provisioning (Schwartz 1994), and what was the nature of these ties (McCorriston 1995)? These early 3rd millennium farming settlements are of particular interest when contrasted with preceding farming strategies, for it is in the early 3rd millennium BC contexts that *Carthamus* first appears.

Archaeobotany in the middle Habur

Archaeobotanical techniques - sampling archaeological sites for charred plant remains from past human economic activities - document prehistoric developments in agriculture along the middle Habur River. By extracting plant remains from many sites (there are now more than a dozen under analysis), this approach has allowed a comparison between different settlements and different time periods. The preliminary results on which this paper relies come from five sites along the middle Habur River and are from rich midden samples containing more than 150 different taxa and types. In analysis the taxa and types have been grouped into categories that reflect where plants were growing (ecology) and what people did with them (economic categories). This approach has therefore distinguished between plant remains from the steppe, riverbank, dry farming weeds, for example, and wheat-threshing debris, barley-threshing debris, wheat grain, barley grain, lentils and other legumes.

The five sites offer a noncontinuous sequence of occupation and farming strategies (McCorriston 1995) that may be summarized as follows.

Umm Qseir, settled in the 5th millennium BC, was a small settlement occupied year-round by pioneering Halaf farmers who relied on a fairly low-risk strategy of hunting wild game from the steppe, raising pigs that could be counted upon to reproduce, tending crops close by the river, and exploiting wild nuts and berries (McCorriston 1992; Zeder 1994). Most samples are dominated by wheat-threshing debris and wheat grain, indicating that the Halaf inhabitants cultivated emmer wheat, a cereal which may be parched to release the grain and as a consequence, generates relatively large amounts of burned chaff in sites. Umm Qseir lacked commensurate charred barley chaff although barley grain was ubiquitous. So were legumes, which were also proportionately very abundant in samples from Umm Qseir. Lentil, pea, chickpea and vetch represent a rather diverse set of crops. These crops were most probably grown on the richest alluvial soils that received some fall flooding in discrete niches along the river, and occasional finds of species that thrive in such habitats (e.g. *Portulaca oleracea*) support this interpretation. The Umm Qseir farmers appear to have planted a wide diversity of crops in a rather narrow, safe niche for farming and collected wild resources such as wood fuel, nuts and berries.

Ziyade is a site only a few hundred yards downstream where subsequent and more substantial occupation during the late 5th and early 4th millennia BC left midden deposits that are still being analyzed. Preliminary results suggest that inhabitants retained most of the crops favored in the preceding period, but they expanded their activities and their uses of the landscape around them in important ways. Wheat-threshing debris, probably mostly from emmer wheat, was a major component of most samples, followed by legumes which, where present, tended to dominate samples. Barley-threshing debris is now present in most samples, suggesting a shift in the processing of the barley crop. Also new at Ziyade is a range of wild plants from the steppe and plants that grow on fallow/steppe soils. These species strongly indicate a new interest in the resources of the steppe, most probably as grazing land near the site for domesticated animals - wild animals still dominate the fauna recovered from archaeological contexts (Zeder, pers. comm.). Burning dung fuel gathered from domestic animals would best explain the incorporation of barley-threshing debris and steppe species into midden deposits.

Dramatic changes in farming strategy accompanied the settlement shift at the beginning of the 3rd millennium BC. Samples from three sites have provided information not only on the charred remains discarded in middens during this period but also on the stored contents of architecturally distinct granaries during their use. On the banks of the Habur River, the sites 'Atij and Raqa'i were founded de novo with grille buildings (granaries) in the earliest levels and substantive, non-domestic architecture, including central granary-type storage buildings, in later levels (Fortin 1990, 1995; Schwartz 1993-1994). The occupants of these sites clearly pursued new farming strategies, and the drop in wheat grain and wheat-threshing debris, along with a dramatic rise in both proportions and ubiquity of barley-threshing debris, points to a new emphasis on this crop and new processing routines that led to incorporation of the chaff in archaeological middens.

The occupants of these 3rd-millennium sites apparently placed great emphasis on a barley crop, so much so that most of the legumes disappear and the range of legumes present has narrowed to exclude vetch and chickpea. Evidence for emmer wheat is also no longer widely attested. This focus on fewer crops, however, was accompanied by a widened use of arable land. Both dry-farming weeds[1] and fallow/steppe[2] indicators are widely attested and in many samples, proportionally abundant. These indicators stem from the new practice of dry farming on the steppe soils away from the optimal yet limited alluvium of the lower river terraces.

> [1] A category that includes *Silene conoidea, Gypsophila pilosa, Vaccaria pyramidata, Euclideum syriacum, Malva* sp., *Asperula arvensis, Centaurea hyalolepis, Cichorium pumilum, Garhadiolus angulosus, Muscari/Ornithogalum* type, *Bellevalia* sp. and *Taenitherium crinitum.*

> [2] Fallow/steppe includes small legumes such as *Astragalus* type, *Medicago radiata, Coronilla scorpioides, Trigonella-type,* and *Aegilops* grains and chaff. These types may incorporate several different plants; moreover, a number of taxa in these genera have broad ecological tolerances in disturbed areas, including fields, on the steppe. Therefore they have been assigned to fallow/steppe and may actually overlap with the steppe and dry-farming weed categories.

Another ecological category includes charred seed remains from wild steppe[3] species, altogether absent at the pioneering settlement of Umm Qseir but ubiquitous thereafter. The middens at 'Atij and Raqa'i were proportionally dominated by these species, which with fallow/steppe probably derived from extensive use of dung fuels at the sites. This represents an indirect yet dramatic indication of a new subsistence focus in the 3rd millennium BC, an emphasis on raising sheep and goats on the lush steppe lands along the middle Habur. Evidence from faunal remains corroborates this shift (Zeder 1995), and it seems likely that animals were fed barley by-products during part of the year and were grazed on open steppe and dry-farmed field stubble at other intervals. Barley-threshing debris was a valuable fodder when other sources were unavailable or restricted.

> [3] Plants such as *Atriplex leucoclada, Salsola/Noaea/Hammada* type, *Hypercoum* sp., *Reseda* sp., *Prosopis farcta, Euphorbia densa, Andrachne telephioides, Haplophyllum tuberculatum, Lygia pubescens, Anisociadium orientale, Androsace maxima, Arnebia decumbens, Teucrium polium, Ziziphora* sp., *Scrophularia* sp., *Crucianella exasperata, Anthemis wettsteiniana, Artemisia herbaalba, Eremopyrum bonaepartis* and *Stipa* sp.

Kerma is an early 3rd millennium BC site with at least one granary that burned with its stored contents intact (Saghieh 1991). The charred plant remains from Kerma are therefore those that people intended to consume rather than to discard, and as such they shed invaluable light on the range of economic activities in the middle Habur at this time. Most notably, the contents of Granary A consisted of clean, threshed hulled-barley grain and grain-shaped, dry-farming weed seeds that had survived threshing and winnowing.[4] The Northern Granary, on the other hand, contained a mix of threshing by-products from barley crops, emmer wheat (*Triticum dicoccum*) and free-threshing macaroni wheat (*Triticum durum*). These also would offer useful fodder, although macaroni wheat is poorly represented in middens. Macaroni wheat would have provided a hardy, lower-risk crop on marginal steppe soils, for it is well suited to dry farming in arid conditions.

> [4] Especially *Fumaria* sp., *Hordeum spontaneum, Bupleurum lancifolium* and Torilis-type.

> [5] No earlier finds of *Carthamus* have been reported. *Carthamus,* not certainly identified to species, also appears in mid-late 3rd millennium BC deposits at Selenkahiye (van Zeist and Bakker-Heeres 1985) and mid-late 3rd millennium BC deposits at Hammam et-Turkman (van Zeist *et al.* 1988).

The plant remains corroborate other evidence that 3rd millennium farmers and herders focused on a narrow range of resources as they became increasingly integrated in a wider pattern of inter-regional exchange and interdependency. A primary focus of farming, barley provided fodder for herd animals raised in great number to provide a surplus of meat or wool products for urban regions. During the spring and early summer, these animals could be grazed on the steppe and on harvested or fallow fields. During winter months, water shortages in the steppe restricted their access and supplemental feed would have been critical for animals too numerous to be supported by vegetation along the river. In summary, the crop base narrowed, arable land use expanded to use the steppe soils, and people organized themselves to produce surplus animals and animal products within a regional exchange network.

Carthamus seeds and *Carthamus* domestication

In this economic and social context, *Carthamus* first appears at 3rd millennium 'Atij, Raqa'i and Kerma (Fig. 2 and Fig. 3, respectively).[5] All three sites yielded samples in which a few seeds or achene shell fragments from *Carthamus* were present as minor components of assemblages with hundreds or thousands of identifiable plant fragments. While it may be difficult to assign shell fragments unequivocally to species, the intact achenes may eventually be further identified. They are 4-5 mm in length and include examples of two types, either dimorphic outer and inner achenes or separate species. Archaeobotanical identifications rely almost exclusively on morphological characteristics for identification since charring destroys seed color, genetic material and behavioral aspects of traits such as dehiscence and dormancy. The archaeological specimens closely resemble several modern reference collections of *Carthamus tinctorius* L., domesticated safflower, but at present reference material from wild *Carthamus* collections in the Jezireh is limited and firmer identification cannot be made without examining such material. Nevertheless, at least one specimen from Tell 'Atij more closely matches collections (from Jordan) of wild *Carthamus tenuis* (Boiss. & Bl.) Bomm. This underscores the possibility that more than one species of *Carthamus* may be represented in the few early 3rd millennium BC specimens at hand.

The origins of *Carthamus tinctorius* L. remain unknown. Genetic research suggests the Euphrates basin as an origin for the crop, and several of the closest modern genetic relatives to safflower grow in Syria today. These are *Carthamus flavescens, C. oxyacanthus* and *C. palaestinus* (Smith 1996). *Carthamus flavescens* only appears as a field weed among summer crops (Sauerborn and Sauerborn 1988) while *C. oxyacanthus* grows wild in the steppe east of the middle Habur (Mouterde 1983). Today domesticated safflower is prized for its oil-bearing seeds and for the yellow dye in its flowers, but its earliest uses remain obscure and an understanding of selective pressures that led to its domestication remains speculative. Changes in seed morphology (which can be detected archaeobotanically) would most likely occur as a

direct result of selecting larger seeds with meats rich in oil and thin walls for crushing. Harvesting immature flower heads for dye would not select for larger, thin-walled seeds.

Other changes in *C. tinctorius* probably also included a reduction of seed dormancy. Although typical cultivars sprout in springtime and grow throughout summer, seeding in August (in mediterranean and continental climates) (Knowles 1955; Smith 1996), there are some winter annuals that lack any seed dormancy and are planted in autumn shortly after seed is harvested (Smith 1996). The former habit is almost certainly the ancestral one, for wild *Carthamus* species are summer-flowering annuals, as are weedy species in summer crops. Loss of seed dormancy most probably was a secondary trait acquired relatively late in *Carthamus* domestication when cultivars were introduced into new climates. Therefore we may infer that the 3rd millennium BC *Carthamus* seeds from the middle Habur were also summer annuals and must have fitted accordingly into prehistoric agricultural cycles.

If *Carthamus* was deliberately sown, this might signal summer cropping, an intensive agricultural practice that extracts several crops each year from a single field. Planting dates for safflower in late winter/early spring preclude this possibility in the Jezireh, where traditional winter cereals and legumes would still be maturing at safflower planting time. Nevertheless, extensive agronomic experience with safflower in mediterranean and continental zones of the United States demonstrates its suitability in crop rotation with wheat and barley on fields that are periodically fallowed (Knowles 1955). Safflower cultivation serves to control weeds, does not deplete the soil as much as a cereal, and volunteers are not strongly competitive in the next cereal planting. Deliberate planting of domesticated safflower would fit into a winter crop/fallow/summer crop rotation in the Jezireh.

Fig. 2. Modern seeds of domesticated *Carthamus tinctorius* L. Seed size and shell thickness have been selected for oil extraction. Note smooth and rugose achenes.

Fig. 3. Charred seeds of *Carthamus* sp. from archaeological deposits at Tell 'Atij and Tell Kerma. Although these resemble wild species, relatively recent selection for oil production has greatly affected the appearance of modern domesticated *Carthamus tinctorius* L.

Furthermore, domesticated safflower has a deep taproot and drought-resistant qualities that would suit it for cultivation in the middle Habur. It thrives in marginal dry-farming regions with a minimum of 250 mm rainfall, yet does not do particularly well under either irrigation or rainfall at maturation (Smith 1996). Residual moisture in deep soils is critical to a safflower crop. If it was actually cultivated along the middle Habur, safflower might indicate greater spring and possibly some early summer rainfall during the early 3rd millennium BC, although this seems a tenuous conclusion at present.

Since the *Carthamus* seeds from 3rd-millennium BC sites cannot be definitively identified as domesticates, the critical question seems to be whether *Carthamus* was deliberately cultivated at all and for what purpose. It is plausibly excluded as a field weed since no summer crops in which it might have grown have been found; similarly, *Carthamus* lacks an obvious partner for intercropping, which limits disease and insect predation. Traditional agricultural practices include its use as an animal feed in China where non-spiny varieties leave field stubble and as a spiny border crop in India where the thorny leaves and stalks exclude animals that might graze cereals (Knowles 1955; Smith 1996).

If *Carthamus* - wild or domesticated - was cultivated in this manner at 'Atij, Raqa'i and Kerma, it might have provided useful barriers in early summer when animals returned to the Habur River (Fig. 4). The appearance of *Carthamus* seeds in 3rd millennium BC middens suggests an association between the plant and the new farming and herding strategies employed at this time. Seeds would be produced in late summer, but the dye-bearing flowers would be available in midsummer during the very season when wool would be sheared and processed near the river. Eventual selection for seed oil content and easier extraction would have ultimately increased seed size and decreased shell thickness. These trends could be measured in appropriate archaeological remains of *Carthamus.* But selection of the plant for its dye (a product of the flower, which is unlikely to preserve archaeologically) or its manipulation as a cultivated, dye-yielding barrier around fields, would not result in morphological changes to the seed.

It is entirely plausible that the plant was first manipulated and used by humans for these purposes; both an emphasis on animal wool production from the 3rd millennium BC onward and the concentration of grazing animals near the river suggest it. Unlike flax fiber, which preceded wool as a major textile fiber in the Near East, wool readily takes a dye, and with the production of wool textiles, people were developing an active interest in dyes and dyed garments. For example, shell- processing in the Persian Gulf for red dyes intensified in the mid-2nd millennium (Edens 1994). *Carthamus tinctorius* flowers yield a yellow dye with simple water extraction.

Fig. 4. Modern field margin with ungrazed stand of thistle *Notobasis syriaca* (L.) Cass. near the Habur River. Sheep and goats pass along this route daily.

Conclusions

The evidence from the middle Habur emphasizes the ongoing changes and adaptations with the development of agriculture and introduces a context for Syrian origins of *Carthamus tinctorius.* The earliest manipulation and cultivation of this plant almost certainly was not for safflower oil, a later attractive quality of the crop, but for dye and as a convenient, thorny barrier protecting fields from grazing animals. When considered in the broader setting of expanding human use of the steppe, its vegetation for grazing domesticates and its soils for raising grain and fodder, the earliest use of *Carthamus* can more clearly be understood. Genetic evidence pointing to its origins in Syria strengthens this argument, and this case offers, once again, a useful interdisciplinary perspective on origins of agriculture.

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Part 6. Conservation of Wild Progenitors

Current Geographical Distribution and Habitat of Wild Wheats and Barley - J. Valkoun, J. Giles Waines and J. Konopka

Introduction

A comprehensive knowledge of the current geographical distribution and habitat of wheat and barley progenitors and close ancestors is important not only for plant scientists but also for archaeologists. The maps of wild wheats and barley distribution by Harlan and Zohary (1966) and Zohary and Hopf (1988) have been the most comprehensive and frequently cited sources of information. Johnson (1975) was probably the first who provided maps of geographical distribution of all four wild *Triticum* species. However, recent changes in the taxonomic concept of wild wheats and additional information on wild wheats and barley distribution obtained in numerous collecting and/or survey missions to Near East countries call for the production of new updated maps of wild progenitors, ancestors and close relatives of cultivated wheats. The choice of species for the maps was based on their relevance to the discussion on wheat and barley origin and domestication.

Material and methods

In this paper, the nomenclature and taxonomic concept of wild *Triticum* and *Aegilops* species is based on van Slageren's monograph (van Slageren 1994), the scientific names and classification of cultivated wheats follow the concept of Dorofeev *et al.* (1979). The following wild wheat species are recognized and treated in the present paper: *Triticum baeoticum* Boiss. emend. E. Schiem. (syn. = *T. boeoticum*) (= *T. monococcum* L. subsp. *aegilopoides* (Link.) Thell.), *Triticum urartu* Tumanian ex Gandilian, *Triticum dicoccoides* (Koern. ex Asch. & Graebn.) (= *T. turgidum* L. subsp. *dicoccoides* (Koern. ex Asch. & Graebn.)) and *Triticum araraticum* Jakubz. (= *T. timopheevi* (Zhuk.) Zhuk. subsp. *armeniacum* (Jakubz.) van Slageren). Other species presented in the distribution maps are: *Hordeum spontaneum* C. Koch (= *H. vulgare* subsp. *spontaneum*), *Aegilops speltoides* Tausch, *Aegilops searsii* Feldman & Kislev ex Hammer, *Aegilops bicornis* (Forssk.) Jaub. & Spach and *Aegilops tauschii* Coss.

The maps were based on the information in the 'Global database of wheat wild relatives' developed by IBPGR in 1990, now upgraded by and maintained at the Genetic Resources Unit of ICARDA (18,000 entries, data from 52 genebanks). Additional information was obtained in 50 collecting and/or survey missions conducted by ICARDA in collaboration with the respective national programs to Syria, Jordan, Lebanon, Iraq, Iran, Turkey, Armenia, Cyprus, Egypt, Libya, Tunisia, Algeria, Morocco, Bulgaria, former USSR, Turkmenistan, Uzbekistan, Pakistan and Tajikstan. Geographical coverage is limited to the Near East region, which is most relevant to the discussion on wheat and barley domestication. Data for Palestine were not available.

Results and discussion

Wild barley

In barley, there is growing evidence that both two-row and six-row forms of cultivated barley originate from a common wild progenitor, *Hordeum spontaneum* C. Koch (Zohary and Hopf 1988). Remains of two-row cultivated barley have been recovered from Pre-Pottery Neolithic A (PPNA) sites (ca. 10,000 BP), while six-row cultivated barley has been found somewhat later, in Pre-Pottery Neolithic B (PPNB) sites (Willcox 1991). Figure 1 was produced using only ICARDA database information, because no global database was available. Consequently, there is a concentration of wild barley sites in the western part of the Near East arc, to which most ICARDA survey or collecting missions were targeted. *Hordeum spontaneum* is better adapted to low-rainfall conditions and less-fertile soils than wild wheat, as is indicated by its presence in the dry sites of central Syria, northern

Jordan and northern Iraq.

Wild diploid wheats

Most treatments on geographical distribution of wild einkorn do not recognize the existence of two wild diploid wheats, *T. boeoticum* and *T. urartu.* However, there has been growing evidence indicating that the two forms are not only separated by crossing barriers (Johnson and Dhaliwal 1976) but they also differ in plant morphology (Gandilian 1972; Dorofeev *et al.* 1979) and biochemical and molecular markers (Jaaska 1974; Johnson 1975; Dvorák *et al.* 1988). Moreover, as Figures 2 and 3 show, they differ in their geographical distribution. *Triticum urartu* is present in Jordan and the Hauran and Jebel Al Arab region in southern Syria, while the species is missing west of the Near East arc. In general, *T. urartu* geographical distribution resembles that of *T. dicoccoides* (Fig. 4) to which it donated the A genome (Dvorák 1976). Sites of *T. boeoticum* are concentrated in southeastern Turkey, where this species was probably domesticated (Heun *et al.* 1997). The current distribution indicates that its weedy races have spread with cultivated cereals far to the west and east.

Wild tetraploid wheats

The two wild tetraploid wheat species - *T. dicoccoides* and *T. araraticum* - are relatively similar in plant morphology, but they differ in their genomic constitution: AABB in the former and AAGG in the latter. Cultivated emmer [*Triticum dicoccum* (Schrank) Schuebl.] was domesticated in the Near East from the wild emmer wheat (*T. dicoccoides*) some 10,000 years ago and, somewhat later, durum and bread wheats were derived from this first cultivated wheat (Zohary and Hopf 1988). *Triticum araraticum* was probably also domesticated but its cultivated form, *Triticum timopheevi* (Zhuk.) Zhuk., was found to be grown in a small area in western Georgia together with its hexaploid derivative *Triticum zhukovskyi* Menabde et Erizjan and cultivated einkorn, *Triticum monococcum* L. (Dorofeev *et al.* 1979).

Geographical distribution of *T. dicoccoides* and *T. araraticum* is presented in Figures 4 and 5, respectively. The two species are sympatric in the northern and eastern parts of the Near East arc and the *dicoccoides* wheat is most frequent in its southwestern region, where the *araraticum* wheat is absent. On the other hand, the distribution of the latter species extends to Transcaucasia, while *T. dicoccoides* does not occur north of southeastern Anatolia of Turkey. The absence of *T. araraticum* in Palestine, Jordan and southern Syria may be significant in the discussion on the origin of cultivated tetraploid wheats.

Fig. 1. Distribution of *Hordeum spontaneum* sites in the Near East region.

Fig. 2. Distribution of *Triticum boeoticum* sites in the Near East region.

Fig. 3. Geographical distribution of *Triticum urartu* sites.

Fig. 4. Geographical distribution of *Triticum dicoccoides* sites.

Fig. 5. Geographical distribution of *Triticum araraticum* sites.

Fig. 6. Distribution of three *Aegilops* spp. sites in the Near East region.

***Aegilops* species**

As no wild hexaploid wheat has been found, bread wheat (*Triticum aestivum* L.; genomic constitution = AABBDD) probably originated from a cross of a cultivated tetraploid wheat and a goatgrass (*Ae. tauschii*) donor of its D genome. Recent evidence indicates that this may have happened in southwestern Caspian (Dvorák *et al.* 1997). Some diploid *Aegilops* species display a very characteristic pattern of geographical distribution (Fig. 6), which reflects their specific adaptation to different ecological zones. Presently, *Ae. tauschii* geographical distribution covers a very large area extending from central Syria in the west to China in the east. Nevertheless, the highest concentration of sites is in Transcaucasia, West Azerbaijan province of Iran and in the Caspian region of Iran. This might have been the original core of the species distribution, from which its weedy races spread with wheat and barley cultivation to the east and west. The genetic diversity data support the assumption that the southern or southwestern coast of the Caspian Sea might be the center of *Ae. tauschii* origin (Lubbers *et al.* 1991; Dvorák *et al.* 1997).

Both *Ae. speltoides* and *Ae. searsii* have been frequently suggested as donors of *T. dicoccoides* B genome. The geographical distribution and ecological adaptation of *Ae. speltoides* mostly coincides with that of *T. boeoticum* and both species may be the dominant components of grasslands on basaltic soils in southeastern Turkey. *Ae. speltoides* is also similar to *boeoticum* wheat in being absent in Jordan and in the Hauran region and Jebel Al Arab of southern Syria. *Ae. searsii,* another putative donor of the wild emmer B genome, is sympatric to *T. urartu*

in Jordan, southern Syria and Lebanon and its geographical distribution and ecological niche are distinct from *Ae. speltoides.*

The current geographical distribution of the wild wheats and barley has a different pattern from that at the onset of agriculture. As cultivated wheat and its wild progenitors and/or ancestors are similar in their ecology, land cultivation resulted in habitat fragmentation and gradual habitat loss in large areas of the Near East. Moreover, the original habitat of wild cereals was also destroyed or modified by other detrimental activities related to human population growth in the Near East region. Therefore, the remaining wild cereal population sites are mostly disturbed and degraded by animal overgrazing. On the other hand, the current distribution area may be larger than 10,000 years ago, because the wild species were spread as admixture with seeds of cultivated species and some of them, like *H. spontaneum, T. boeoticum, T. urartu* and *Ae. tauschii,* developed weedy races, well adapted to growing in cereal fields. Consequently, diploid wheat species, *T. boeoticum* in particular, occupy a larger geographical area than tetraploid wheat species, *T. dicoccoides* and *T. araraticum,* which are not weedy.

The maps by Harlan and Zohary (1966), Johnson (1975), Zohary and Hopf (1988) and some others have already contributed to the discussion on the wheat and barley domestication. Nevertheless, the new data presented in this paper on the current geographical distribution of wild progenitors and close relatives of wheat and barley, two 'founder' crops of the Neolithic revolution, may still be useful in the discussion on the origins of agriculture in the Near East.

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In situ Conservation of Wild Relatives of Crop Plants in Relation to their History -

J. Giles Waines

Introduction

A useful distinction when thinking about the events and processes in the past is the difference between history and prehistory (Barfield 1967). History encompasses those events that humans perceived and recorded either through writing or art, whereas events that humans may or may not have perceived, but did not record, fall into the realm of prehistory. This distinction places most of the events in plant and animal domestication and crop evolution in prehistory, which implies that there may be difficulty in knowing exactly what happened because these events took place such a long time ago and were not interpreted at the time by humans. When we think of *in situ* conservation of the wild relatives of our crop plants in relation to their history we should insert 'prehistory' into the title. Further, the word history in the title can have several different meanings, depending on whether we think of the history of the crop plant or the interaction of the plant with the history of humans.

Genetic prehistory

Thinking of the prehistory and history of the plant in a genetic sense and taking durum wheat as an example, we believe that this wheat was selected from *dicoccum* or emmer wheat, which was domesticated from wild tetraploid populations of emmer, namely *Triticum turgidum* L., subsp. *dicoccoides* (Körn. ex Asch. & Graebn.) Thell. about 10,000 years ago (Zohary and Hopf 1993). Today there are still primary stands of wild emmer at various locations in the Fertile Crescent, and some of these should be conserved *in situ.* Populations I have seen include the extensive stands in the Jebel Druz in southern Syria, where the wild relative may also grow with diploid *T. urartu* Tum, ex Gand. On the drier eastern side of the Jebel Druz, *T. urartu* grows alone. A population should be conserved from northern Syria, possibly the Der Jamal site in Aleppo province. This population includes wild emmer (*T. urartu*) and wild einkorn [T. *monococcum* L. subsp. *aegilopoides* (Link.) Thell]. At a site near San Simeon monastery, Aleppo province, the other wild tetraploid wheat [*T. timopheevii* (Zhuk.) Zhuk. subsp. *armeniacum* (Jakuz.) van Slageren] is found, and this would be a prime area for *in situ* conservation. If wild tetraploid wheats are found growing in northeastern Syria, in Hassakeh province, that site should also be conserved. Lebanon has several populations of wild emmer worth conserving. These include that at Rashayya in the south Beka'a Valley, where wild emmer was first collected at the end of the 19th century, and there are several locations in oak-park forest habitats flanking the central Beka'a Valley, where primary populations of wild emmer appear to thrive. I stress the need to conserve primary populations in old established habitats rather than weedy secondary populations along roadsides, which may show a strong founder effect and exhibit little genetic polymorphism. An example of a secondary population in *Aegilops speltoides* Tausch. might be the roadside population northwest of the village of Abeen in Aleppo province, Syria, whereas a more primary population might be that at Ain Diwar in Hassakeh province (Waines *et al.* 1998). With reference to einkorn, we also need to preserve populations of wild einkorn from the extremities of its range, which extends from southeastern Europe to the Caucasus and south into Lebanon, Syria, Iraq and Iran, and northward into the Crimea.

Evolutionary prehistory

Tetraploid wild emmer (BBAA) has its own evolutionary prehistory. This is currently interpreted as being the result of a cross between a wild diploid goatgrass (BB) similar to *Ae. speltoides* (SS), which was the female parent, with wild *T. urartu* (AA) as male parent (Dvorák and Zhang 1990). Hence primary populations of all three species need to be conserved *in situ.* However, the two diploid species and the derived hybrid allotetraploid occupy different habitats and have different ecological requirements, especially for minimum amounts of rainfall. For example, *Ae. speltoides* requires more precipitation than *T. turgidum* subsp. *dicoccoides,* whereas *T. urartu* extends farther into the drier areas than the other two species. Although we do not know what climatic conditions were like tens of thousands of years ago, the three species grow together only rarely today. The population between Kilis and Gaziantep in Gaziantep province, Turkey, is one that springs to mind. This population also has the other allotetraploid wheat species *T. timopheevii* subsp. *armeniacum,* which has a female parent genome designated (GG). This genome is also considered to have come from *Ae. speltoides,* perhaps at a later date than the (BB) genome. There are several translocation differences between the (BB) and (GG) genomes (Feldman 1966).

As *Ae. speltoides* was the female genome donor to both emmer and timopheevi wheats and provided the chloroplasts and mitochondria to the polyploid wheats, it has been argued that more effort should be made to conserve this species *in situ,* than either *T. urartu* or *Ae. tauschii* (DD) (Waines *et al.* 1997).

The DD genome of bread wheat is known to have been contributed by *Ae. tauschii,* a diploid goatgrass native from near Russafeh, Raqqa'a province, in the Syrian Desert to western China. A population is also known from the western side of the Ceylanpinar State Farm in Urfa province, Turkey. The annual precipitation at Russafeh averages 150 mm, but *Ae. tauschii* grows in cereal fields in depressions left by the meandering Firat River, so

these areas may receive winter runoff, and the actual water available may be more. *Aegilops tauschii* is thought to confer ecological adaptability to bread wheat, which is more tolerant to drought, cold and heat than durum wheat, quite apart from genes for bread-making, and disease and pest resistance. *Aegilops tauschii* should be conserved *in situ* in these dry desert regions, as well as in wetter sites in northwestern Iran, where the actual parent of bread wheat may have grown (Dvorák *et al.,* this volume).

Soil types and animal predators

Many wild cereal populations thrive in basalt soils or around piles of basalt rocks collected when fields are cleared. These rocks seem to protect the plants from grazing animals. Soil types are important for wild cereals, and populations that thrive on basalt, terra rosa, alluvial and possibly serpentine soils are known. The degree of soil cracking as fields dry out in summer is important, for spikelets and spikes can be protected in the cracks from predation by seed-harvesting ants, rodents and fire. There is little information from the Near East on the extent of predation by insects, animals and fungal diseases on fruits and seeds of wild relatives of cereal and legume crops. Nor do we have much information on overgrazing of wild cereal stands by sheep, goats and cattle. Harvester ants of the genus *Messor* may be important in gathering and disseminating wild cereal grains in specific areas of the Near East such as Israel and Syria. Rodents of unknown genera have been observed to harvest wild wheats and goatgrasses in Syria in the Jebel Druz and Jebel Abd-el-Aziz, respectively. At the latter site, *Ae. crassa* spikelets were collected and transported to threshing mounds. Clearly, harvester ants and small rodents may be a force that selects for wild wheat inflorescences that disarticulate at maturity. Larger rodents may harvest and select for goatgrass inflorescences that remain entire.

The agricultural system

History can also apply to the crop and the agricultural system in which it is farmed. An example is the areas of north-central Turkey where landraces of einkorn (*T. monococcum* subsp. *monococcum*) and emmer [*T. turgidum* subsp. *dicoccum* (Schrank) Thell.] wheats are still grown for animal and/or human food. The village of Sabace in Kastamonu province still grows landraces of these ancestral hulled wheats (Karagöz 1996; Nesbitt and Samuel 1996). Several villages in northern Morocco still grow einkorn wheats. We need ethnographic information on why these landraces are still grown, and we need to explore ways of preserving *in situ* the agricultural systems that include these landrace crops.

Endemic wild systems

Chickpea, *Cicer arietinum,* presents an interesting contrast to einkorn. As far as we know, chickpea was domesticated from wild *C. arietinum L.* subsp. *reticulatum* Ladiz., which has a very restricted area of distribution. It is known only from the provinces of Adiyaman, Mardin and Siirt, in southeastern Turkey and grows on limestone-derived soils (Zohary and Hopf 1993). A closely related species, *C. echinospermum* Davis, grows on basalt-derived soils in Urfa, Diyarbakir and Mardin provinces of southeastern Turkey and in the Jebel Sinjar in northern Iraq. Both species are able to exchange genetic material with *C. arietinum* subsp. *arietinum,* but in the case of *C. echinospermum,* there are some sterility barriers. Thus, the fourth most important pulse crop in the world, which has many landraces and modern cultivars in five continents, was domesticated from a wild species endemic to Turkey with a very small area of distribution. Surprisingly, although cultivated chickpea is so valuable a protein crop for humans, there appear to be no extant efforts to conserve wild populations *in situ* in southeastern Turkey. There is a need for the Turkish Government and IPGRI to develop a plan for *in situ* conservation of this valuable germplasm. Further, there appear to be few studies of the population biology of wild *Cicer* plants in its area of endemism; we do not know how extensive these wild populations are. I realize that these provinces in southeastern Turkey are politically unstable, but germplasm preservation of wild chickpea, the provider of 'hommous', is a subject that might find support from all people.

Widespread wild systems

Tepary bean, *Phaseolus acutifolius* A. Gray, affords a second example of a legume with a small area of domestication in a species with a wide distribution. Tepary grows wild from Arizona and west Texas south to northern Guatemala. There are two botanical varieties: *acutifolius* and *tenuifolius.* The former grows in valley bottoms, and the latter, with narrow leaves, grows on valley sides. The leaf and seed size characteristics are inherited. It is thought that the larger seed of var. *acutifolius* was that chosen by native Mexicans for domestication. All domesticated forms have a rare duplication of an enzyme locus, which only occurs in Sinaloa or Jalisco, Mexico (Garvin and Weeden 1994). This pinpoints domestication of tepary to probably a single act in Sinaloa or Jalisco, which spread later as a cultigen northward into Arizona and southward into Nicaragua. Wild populations in Sinaloa and Jalisco expressing the duplication should be conserved *in situ,* as should also populations from the extremities of the range of the wild species. In Arizona, many of the *tenuifolius* populations grow in the National Forest, so as long as the forest is protected, the wild teparies will be also.

Multiple sites of domestication

Common bean, *Phaseolus vulgaris* L., presents an interesting example of possible multiple locations and times of domestication (Gepts *et al.* 1986). Common bean grows wild from southern Sonora, Mexico, to northern Argentina. There are two subspecies: *sylvestris* in Mexico and Central America, and *aborigineus* in South America. These were domesticated in Mexico and South America, respectively, giving rise to the Mexican and South American genepools of domesticated common beans. It is possible that there was more than one domestication of wild beans in Mexico, giving rise to the Jalisco, Durango and other cultivated races from Mexico, all of which have distinguishing molecular and phenotypic characters (Singh *et al.* 1991). If this is the case, wild populations representative of all the domesticated races should be conserved *in situ.*

Sacred groves

Forest trees were also important in the development of Near Eastern agriculture and civilization. In Lebanon there are one or two groves of the native cedar of Lebanon, *Cedrus libani* L. A sacred grove in Bsharri in the Lebanon Mountains is associated with a chapel. By preserving the cedar trees in this grove, other species are also conserved *in situ,* such as *Secale montanum* L., *Vicia* species and the beautiful, white-flowered ornamental *Salvia microstegia.* Sacred groves are common in forested areas in the Eastern Mediterranean countries and in other areas such as India and West Africa, and they may constitute small but important *in situ* conservation sites (Lebbie and Guries 1995; Nair *et al.* 1997).

Archaeological sites

Archaeological sites may also act as good *in situ* conservation areas. The dead Byzantine cities in northern Syria are important archaeologically. Some of the buildings are intact, others were toppled by earthquakes. Among the fallen stones, somewhat protected from grazing animals, grow many wild relatives of the Near Eastern complex of domesticates such as *Pisum sativum* L. subsp. *humile* Boiss and Noë and subsp. *elatius* Bieb., and the yellow-orange flowered *P. fulvum* Sibth and Sm., *Lathyrus* species, *Vicia* species, *Lens* species, as well as *Hordeum vulgare* L. subsp. *spontaneum* Koch, *Aegilops, Triticum* and *Avena* species. Several ornamental plants also inhabit these ruins, including wild black iris, which may have had a long association with humans because of their beauty or their association with cemeteries. Clearly protecting ruins also conserves the wild relatives of crop plants, as was suggested for relict cacti in Mexico (Bentz *et al.* 1997).

International borders and military bases

Other areas that can double as an *in situ* conservation site are international border zones. One most relevant is that between northern Syria and southern Turkey. Especially on the Turkish side, there is a strip of land of variable width that is retained as native vegetation, whereas other parts of the zone are farmed. The unfarmed areas may be mined. In the areas that have native vegetation, and which can be seen from the main road outside of the zone, *T. urartu* and *T. monococcum* subsp. *aegilopoides* appear to grow, and I assume that there are other relatives of crop plants.

The Herbarium at the University of California, Riverside, recently undertook a project on a nearby US Marine Corps base in the Mojave Desert to monitor the presence and food source of an endangered species of desert tortoise (*Gopherus agassizi*) which inhabits the base, despite the live shells that explode around it from target practice.

The military of great countries have a vested interest in protecting the natural resources of those countries, especially the relatives of their crops. There appears to be little disturbance to vegetation within the Turkish border zone. In areas rich in the relatives of crop plants, such as the Near East, these border zones can also be recognized to double as *in situ* conservation sites.

Agricultural research stations

A final example for *in situ* conservation sites of either native or introduced species is national or state agricultural experimental stations or state farms. The Ceylanpinar state farm in Urfa province, southeastern Turkey, is being developed as an *in situ* conservation area for wild cereals, legumes and other Near Eastern domesticates by the Turkish Government and the World Bank. This large state farm is located in the northern apex of the Fertile Crescent. The advantage of using state farms is that the state already controls the system of agriculture practised there.

In northern California, the Hopland Field Station in Mendocino County is part of the University of California Agricultural Experiment Station system. The Station is primarily used for rangeland experiments with sheep and other animal-plant interactions. In the 1950s, one field became infested with bearded goatgrass, *Aegilops*

triuncialis L., and this noxious weed has now invaded most areas of the station. At Hopland, this aggressive tetraploid weed is successful because it appears to have no disease, insect or rodent predation. This allows for prolific regeneration and spread by this competitive wild wheat, which is the most widespread of the wheat genepool after durum and bread wheats. Such a situation allows for an excellent study site where the population ecology of this grass can be monitored without the interference that might be found in the Near East. Why are some tetraploid goatgrasses such aggressive weeds? To what extent does the unusual dissemination of the entire inflorescence contribute to this success? A similar mechanism with dissemination of multiple fruits or seeds is found in crops from other families, for example, Chenopodiaceae and Moraceae.

Another example of the usefulness of national agricultural experiment stations to study *in situ* conservation is found in Syria, where cooperation between the Syrian Department of Agriculture and ICARDA has set up study sites in four different ecogeographic areas in the country. The site at Yamuk Experiment Station near Azaz in Aleppo province has allowed for replicated experiments lasting several years, in which wild cereal and legume relatives can be studied in single-species plots or as interactions in multiple-species plots. Similar experiments have been set up at Tel Hadya, south of Aleppo, on a station near the Lebanese border, and on one in the Jebel Druz. There is a need for sites similar to the long-term Rothamsted Park Grass Experimental Field to study *in situ* conservation over many seasons, using many different members of the relatives of Near Eastern crop plants. There is also the ability to study controlled grazing or burning of these *in situ* sites to approximate more exactly the conditions in farmers' fields.

Conclusions

In Turkey and in Syria, experiments are underway to set up and study long-term *in situ* conservation sites for relatives of the Near Eastern complex of domesticated plants. At present, there is a shortage of basic information on population biology and ecology of the several plant and animal species that inhabit primary sites and potential locations for *in situ* conservation. Besides the interactions of wild plants and animals, we need to understand the interaction of these wild species and landraces with modern plant and animal agricultural systems. Considering the large sums that have been spent to understand biodiversity and population ecology of nonagricultural species, it is high time that funds be provided to understand the population biology and ecology of the ancestors of our major crop plants, many of which are native to the Near East.

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Domestication of Cereal Crop Plants and In situ Conservation of their Genetic Resources in the Fertile Crescent - A.B. Damania

Introduction

The evidence for domestication of plants goes back only 10,000 years and 8500 years for animals. Domestication is not an event but a process. Humans seem to have taken an immensely long time to discover the process of obtaining food through plant cultivation. Perhaps food was obtainable in abundance exclusively by hunting, gathering and fishing, hence no need was felt to explore the possibility of cultivation - a relatively more labor-intensive task.

According to a report in the London Times dated October 25, 1995 on the proceedings of a conference on 'Food, People and Health', a suggestion was made that humans should turn the clock back about 15,000 years and eat the diet of the hunter-gatherers in order to maintain good health. The late Palaeolithic diet included relatively lean meat of undomesticated animals, wild fruits and vegetables and nuts, berries and tubers with little or no cereals or dairy foods. It seems this diet matches human metabolic requirements perfectly. According to Professor Boyd Eaton (pers. comm.) communities changed over to agriculture to support a growing population and sustain larger social groups rather than to improve their diet.

The transition from hunting/gathering to agriculture

Smith (1976) suggests that the presence of abundant supplies of wild grains and other resources following favorable post-Pleistocene environmental changes could have led to a 'mini' population explosion in Southwest Asia. Increasingly sedentary lifestyle may have further accelerated population growth through closer spacing of births, a higher rate of infant survival, and perhaps a lower rate of adult mortality. Harlan (1992) maintains that hunter-gatherers have survived until today in places where agriculture is unrewarding.

Several crop plants which have assisted in the establishment of western civilization have their origin in an arc of land that connects the valleys of the Euphrates and the Tigris with the Jordan. This was termed the Fertile Crescent by Breasted (1938).

Besides the evolution of a non-brittle rachis which led to the domestication of wild cereals there is also the fact that persistent glumes made threshing difficult. At what stage after domestication did the cereal spikes develop into free-threshing types so that the grains could be easily obtained? Even today in some of the subsistence farming communities in West Asia and North Africa (WANA), the most primitive methods of separating grains from chaff are utilized such as repeated trampling of harvested stems by horses, mules or donkeys. Hence, it is probable that domestication took place in two stages. The selection for a non-brittle rachis was followed by selection for plants with free-threshing grains from spikelets. In fact, the two most ancient forms of wheats - einkorn and emmer - have persistent glumes on their grains. Their flour and dough properties are very different from those of macaroni wheat (*Triticum durum*) and bread wheat (*T. aestivum*) which evolved several centuries later (Nesbitt and Samuel 1996).

The ancient cereals (the term 'cereal' has its origin in the name of the Roman goddess of plenty: Ceres) such as tetraploid wheat and barley seem to have originated in or near the oak woodland belts in an arc through the hilly country surrounding the Syrian-Mesopotamian Plains (Harlan 1970) between 10,000 and 8000 BP (van Zeist 1969). The study of their domestication is facilitated by the fact that their wild progenitors can still be found in areas which Vavilov considered as their centers of origin (Damania 1990). In southeastern Turkey, northern Iraq

and western Iran (part of the Fertile Crescent) wild wheats and barley are found in the oak forest belt. Archaeobotanical evidence indicates that wild plant species were present on human habitation sites at least 2000 years before the process of domestication began.

Very recent studies on einkorn wheat domestication using amplified fragment length polymorphism (AFLP) show that *T. boeoticum* was domesticated in southeast Turkey in the Karacadag Mountains close to Diyarbakir (Heun *et al.* 1997). However, localization of the precise domestication site of one 'founder crop' through DNA fingerprinting does not necessarily imply that the human hunter-gatherers living there at the end of the Palaeolithic period played a decisive role in establishing agriculture in the Near East. However, charred remains of wild einkorn found at sites on the middle Euphrates, such as Abu Hureyra and Tell Mureybit, downstream from the Turkish location in Syria may have evolved there independently since the climate at that time was conducive to their growth (Hillman 1996).

West Asia, and particularly Syria, has not only been a cradle of human civilization but also includes areas where domestication of wild plants may have first occurred (van Zeist and Bakker-Heeres 1982). By 7000 BP, both wheat and barley had spread to the Harsuna settlements of northern Iraq. The region includes two of the most important Vavilovian centers of origin of food crops - the Near East and the Mediterranean. These two regions fall within the pattern of global genetic diversity also described by Harlan (1970, 1971). The rich regional biodiversity in crop plants and their wild relatives is now threatened by rapid urbanization and overgrazing by small ruminants as flocks are multiplied to satisfy the demands of an increasing human population.

The Neolithic (= food-producing) agricultural development in West Asia depended primarily on the cultivation and subsequent domestication of three species: (1) einkorn wheat (*Triticum monococcum*) domesticated from its wild progenitor *T. boeoticum,* (2) emmer wheat (*T. dicoccum*) domesticated from *T. dicoccoides,* and (3) two-row barley (*Hordeum vulgare* subsp. *disticum*) from *H. spontaneum.* The domestication occurred with the unconscious selection by the early farmer for heads with a non-shattering rachis. The wild mode of seed dispersal gradually disappeared, the wild-type germination of seed on the ground was lost, and there was an increase in kernel size and yield potential (Diamond 1997). The plants which evolved with these traits subsequently lost their ability to survive in the wild.

Small fanning villages have been excavated in the Jordan Valley as well as near Damascus and along the middle Euphrates (Willcox 1996). Over the next 8000 years or so domesticated cereals would provide reliable food sources, thus eliminating the need for people to rely on the wild species that had defined human existence for thousands of years. Further, unlike before, the food grains could be stored for a number of seasons. This led to growth in human population as well as more complex human societies. Today 97% of arable land in WANA is under cultivation with a possibility that human population growth may overtake food production. Crop failures and famines are also an integral part of agricultural systems.

The wild progenitors of cereal crops

Wild einkorn (*T. boeoticum*) (2n=14) occurs across a wide area in the northern portion of the Fertile Crescent, through much of the Anatolian peninsula and penetrates into the southern Balkans. In addition, wild einkorn also occurs as a weed on the borders of cultivated fields and along roadsides. Two main ecogeographic races of *T. boeoticum* have been recognized by botanists. A relatively small one-seeded type typical of the cooler Balkans and Western Anatolia is usually referred to as *T. boeoticum* subsp. *aegilopoides,* while the larger two-seeded race in the warmer dry summer areas of southern Turkey, Iraq and Iran is commonly referred to as *T. boeoticum* subsp. *thaoudar.* In Anatolia all intergradations and intermediates between these two races occur often in mixed stands (Zohary 1969).

Wild einkorn was frequent among the plant remains found at Epipalaeolithic Abu Hureyra on the middle Euphrates and more recently by Willcox (1996) at D'jade. Further south at Tell Mureybit, also on the middle Euphrates, van Zeist and Bakker-Heeres (1984) of the Biological Archaeology Institute, Groningen, Netherlands found strong evidence of the extensive use of wild einkorn as a food source. Both Abu Hureyra and Tell Mureybit sites are now permanently under Lake Assad which flooded them about 20 years ago when the Tabqa dam was built. In 1970 Jack Harlan, in an experiment conducted at the University of Illinois, Urbana-Campaign, showed that a small family could gather enough wild einkorn in only three weeks of hand-harvesting to last a full year (Smith 1995).

Vallega (1996) speculates that *T. boeoticum* and other wild cereals were probably harvested prior to maturity to avoid losses due to brittleness of the rachis. The glumed grains may have been exposed to fire and roasted and eaten as whole kernels or ground into a meal of porridge or made into unleavened flat bread. Even today grains of free-threshing polyploid wheats are harvested while still green and roasted to produce 'frekeh' all over WANA.

Wild emmer (*T. dicoccoides*) is the progenitor of cultivated emmer (*T. dicoccum*). Both the wild ancestor and the

domesticated form have a tetraploid configuration (2n=28), separated by a distinct seed-dispersal biology. Hybrids between them are fully interfertile, thus encouraging continuous gene exchange between the two. Wild emmer has a typical shattering rachis with each spikelet serving as a seed-dispersal unit, whereas in the domesticated emmer the mature ear stays intact and grains are separated from the spikelet only by vigorous threshing. The grains retain their persistent glumes unlike the more evolved *T. durum,* where the grains are naked. In spite of the availability of naked wheats, hulled wheats like emmer were preferred for several thousands of years until about 3000 BP (Harlan 1995). It remains a mystery why hulled wheats dominated over naked ones in several different cultures for a very long time, and in some cases continue to do so right up to the present day.

Hulled wheats were more successful because of their persistent glumes which prevented incidence of fungal diseases such as stem and yellow rusts, to which naked wheats must have been invariably susceptible (Nesbitt 1995). Also, they were ideal feed for poultry and domesticated animals. Furthermore, emmer has a higher protein content percentage (18.6-20.9%), a significantly higher number of total and fertile tillers producing a large biomass, and tolerates poor soil and adverse climatic conditions with little need for the use of fertilizers (Damania *et al.* 1992). But in recent years their area of cultivation is in steep decline, often being restricted to a single field in a mountainous village (Perrino and Hammer 1982).

Vavilov observed that emmer fields were cultivated by Armenians in Persia and by the Basques in Spain and that they were invariably infested with wild oats. Certain Italian farming communities in the Appennine Mountains, using traditional agricultural practices, still grow *Triticum monococcum* (einkorn) and *T. dicoccum* (emmer) wheats. They were extensively grown during Roman times but thought to have disappeared from the peninsula (Perrino and Hammer 1982). With support from the European Economic Community (EEC), efforts are being made to convince these small farming communities to continue to grow these hulled wheats.

Wild emmer has a more restricted distribution than wild einkorn. It is found in Israel, south Syria and Transjordan. Its center is on the slopes of eastern Galilee and the adjacent basaltic plateau of the Golan Heights and the Hauran Plains. In these areas *T. dicoccoides* is fairly common, particularly in places that are not overgrazed by small ruminants. Most recently samples have been discovered growing on basaltic soils in northern Syria, close to the border with Turkey. Robust, early maturing types are found growing in relatively warmer habitats and more slender, later-maturing types are found at higher elevations, e.g. on the eastern slopes of Mt. Hebron.

There is also another form of wild tetraploid wheat, *T. araraticum,* which is found in the former Soviet Transcaucasia, Syria, southeastern Turkey and Iraqi Kurdistan. While *T. dicoccoides* crosses easily with cultivated tetraploid wheats, *T. araraticum* does not, most probably because of the different genomic structure of their chromosomes. The latter shows close genetic affinity with the endemic *T. timopheevi,* a restricted and rare form of cultivated tetraploid wheat found in a single district of Georgia in the former Soviet Union (Zohary 1969). It is probably a more recent domesticate rather than an old relic crop plant from the past (Zohary 1996). Rapid diffusion of both einkorn and emmer wheats from the Fertile Crescent area preempted the widespread cultivation and diffusion of other related domesticated wild grasses, such as *T. timopheevi* (Diamond 1997). It is speculated that when emmer cultivation spread to Transcaucasia, local populations of *T. araraticum* could have grown as a weed of emmer crops and, by being incorporated into the agricultural cycle of harvest and sowing, became domesticated (Nesbitt and Samuel 1996).

Similarly, other lesser-known hexaploid wheat forms such as *T. compactum* or club wheat and *T. spelta, T. vavilovii* and *T. macha* were once grown in Central and West Asia and are found as single-plant volunteers in fields of durum and bread wheat even today. Another hexaploid wheat, *T. sphaerococcum* or shot wheat, originated in India but did not spread. Lesser-known tetraploid wheats such as *T. polonicum,* or Polish wheat, also have a restricted growth area.

Mention must be made here of a form of tetraploid wheat (*Triticum turgidum*) or poulard wheat which is still being grown in the Yemen although it is now rapidly being replaced by varieties of bread wheat mostly introduced from India (Damania *et al.* 1985). Poulard wheat could have been introduced into Yemen from Ethiopia, which is considered by some authors as a center of secondary diversity of tetraploid wheats. The hard poulard wheat samples collected in 1980 and 1981 from the Yemen by missions sponsored by the International Board for Plant Generic Resources (IBPGR) had a high gluten content and were distinguished from durum wheat (*T. durum*) by a pale brown seed color and larger kernel size (Damania 1983). Flour color probably excludes this form of wheat from being used extensively for pasta-making.

Wild barley, *Hordeum spontaneum,* the progenitor of cultivated barley, H. *vulgare,* shows a much wider distribution and over much more diverse types of terrain than wild wheats. The earliest carbonized remains found of cultivated barley are of the two-row type, but six-row morphology appears at Ali Kosh (in Iran) at around 8000 BP (Harlan 1995). Wild barley is found all over the Fertile Crescent where it forms an important annual component of open formations, and is particularly common in the dry-summer belt of the deciduous oak forests,

east, north and west of the Syrian Desert and the Euphrates basin as well as the slopes facing the Jordan Rift Valley (Zohary 1969). In the Fertile Crescent countries H. *spontaneum* is often seen growing on the edges of cultivated fields and roadsides. It is rarely found at higher elevations since it does not tolerate cold very well but is more xeric than the wild wheats and can be found in drier areas of the steppes. Because of its shorter life cycle than wheat, barley can be grown on marginal areas of agriculture. There is abundance of diversity in forms from large-seeded, long-awned types to slender, small-seeded types. Intermediate forms between these extremes are found all over Israel, Syria, Turkey and Iran. Hillman and Davies (1992) and others have shown that low proportions of tough rachides (basal internodes) can occur in assemblages of wild barley and one has to be cautious in using their presence as an indicator of domestication.

In situ conservation of cereal wild progenitors

The ecological amplitude of wild relatives of the three founder cereals may exceed those of the crops derived from or related to them, a feature plant breeders exploit to enhance resistance to biotic or abiotic stresses, thereby increasing the adaptive range of the crop concerned.

Recent pilot studies carried out at ICARDA in Syria (Valkoun and Damania 1992) and elsewhere (Jana 1993) have demonstrated extensive genetic diversity in the original populations of the wild genepool in the natural habitat which is impossible to preserve by the standard *ex situ* collecting procedures. Also, it is generally accepted that during field collection usually only about 50 to 150 plants per site are sampled and many genotypes may be left out. On the other hand, under *in situ* conservation a much larger and continuously evolving genetic diversity is preserved.

Indirect evidence from studies carried out so far indicates that *in situ* methods should be effective for the conservation of genetic diversity in populations of both cultivated and wild species. During their long history of propagation in crop fields in the centers of origin and primary diversity, landrace populations of major crop species were in close association with their wild and weedy relatives. They occasionally exchanged genes, usually at the borders of cultivation, and mutually enriched their genetic diversity (Kuckuck and Pohlendt 1956). They coevolved, during which time they were exposed to a multitude of biotic and abiotic stress selection pressures to which they have adapted themselves as seen in bread wheat (*Triticum aestivum*) fields in Iran (Damania *et al.* 1993).

From biological considerations, the relative merit of the *in situ* method for conserving biodiversity within a cultivated species may be best evaluated in comparison with its wild evolutionary progenitor. Although several comparative studies on diversity in wild and cultivated barley have been reported (Jana 1993), comparable investigations are rare in wheat. In a preliminary assessment of genetic variation in durum wheat (*Triticum durum*) wild emmer (*T. dicoccoides*) populations from Turkey, the results showed that there was no difference in overall genetic diversity between the two.

Germplasm could be repeatedly collected from *in situ* conservation sites for offsite evaluations from time to time. The sites should be exposed to limited grazing periodically in order to maintain soil fertility and prevent it becoming a forest again. An ongoing experiment spanning five years is underway at ICARDA to establish well-defined populations of wild relatives of cereals and legumes conserved *in situ* and thereby determine the main factors which affect survival and competitive ability, and evaluate colonizing ability and regeneration capacity in populations of the target species: *Hordeum spontaneum, Triticum urartu, T. boeoticum, T. dicoccoides, Lens orientalis, L. odemensis* and two annual *Medicago* species and their mixtures. Sheep are allowed to lightly graze the experiments to simulate as far as possible the actual disturbance factors involved in this type of conservation effort.

In wild cereals such as *T. boeoticum, T. dicoccoides* and *H. spontaneum,* selection for a non-brittle rachis led to their domestication. Both wild diploid wheats and wild barley show great climatic tolerance in terms of their natural distribution. Their natural habitats range widely in latitude and altitude. Wild einkorn (*T. boeoticum*), for example, can be found growing from sea level in Macedonia to 2000 m asl in Iran and Iraq. The most dense stand encountered so far has been in southeastern Turkey at altitudes between 900 and 1500 m (Willcox 1992) in the Karacadag Mountain areas. Wild emmer (*T. dicoccoides*) has been reported from 100 m below sea level in the Jordan Valley and at 1500 m on the slopes of Mt. Hermon in Palestine (Zohary 1969). Several of these habitats qualify for consideration as *in situ* conservation sites.

During explorations in Iran, Damania *et al.* (1993) noted that the presence of wild *Triticum* taxa, in areas of their previously reported center of diversity, was extremely limited. This observation is worrisome, not only from the conservation point of view. *Triticum* species are a useful genetic resource since it has been reported that the wild species may provide valuable traits, such as disease resistance and stress tolerance, for wheat improvement. It is recommended that certain sites in Iran be considered for immediate *in situ* conservation to preserve the few remaining populations of wild *Triticum* spp. Later, selected genotypes from these populations can be multiplied

and reintroduced in areas where they were found in abundance in the past.

Monitoring and sampling *in situ* conservation sites

Genetic diversity through the study of seed storage protein (gliadin) polymorphism was carried out on populations of *H. spontaneum*, *T. urartu*, *T. boeoticum* and *T. dicoccoides* collected from the southern provinces of Sweida and Damascus, the Anti-Lebanon Mountains, and the northern province of Aleppo during 1991, 1992 and 1993. Relatively high genetic diversity was found in populations collected from the high plateau in the province of Sweida, while populations found in valleys of the Anti-Lebanon Mountains showed lower diversity (Valkoun and Damania 1992). The discovery of *T. urartu* growing in close proximity with *T. dicoccoides* and *H. spontaneum* in the middle of the Hauran Plain forms a link between the *T. urartu* populations found on the slopes of Mt. Hermon and the Jebel Al Arab Mountains of the Sweida province in southern Syria. This may also indicate that the Hauran Plain used to be the natural habitat of the two wheat ancestors and wild progenitor of cultivated barley before the area came under cultivation and was intensively grazed by sheep and other small ruminants. These wild progenitors could have been even more widespread than today during the Neolithic and there may have been a considerable time lapse between their usage as a food source, i.e. beginnings of cultivation and their actual morphological domestication (Willcox 1996).

Long-term monitoring of biodiversity is essential to develop an understanding of its value for conservation and sustainable use. During 1993 a monitoring trip was conducted jointly with Syrian scientists with the objective of gathering information on these sites (land use, farming system and socioeconomic background, botanical composition of the associated vegetation, etc.), and the target species populations (phenology, reproductive ability, vigor and health). It was observed that the populations of wild progenitors of cereals are relatively well protected from grazing during the vegetative phase when they grow on non-arable habitat among the basaltic rocks. They are inaccessible before the harvest of durum wheat by which time the spikes have matured and shattered on the ground, averting damage from grazing small ruminants. However, when the ownership of the land is not in private hands, flocks belonging to wandering Bedouin tribes graze continuously with deleterious effect on the plants. Only highly unpalatable spiny weeds survive this form of grazing and not a single plant of wild *Triticum* spp. is left standing (Damania 1994).

During these missions *T. urartu* populations were also sampled from the Anti-Lebanon Mountains growing on the borders of orchards, above the summer resort town of Bloudan, at an elevation of 1840 m asl, the highest collecting site reported for this species so far (ICARDA 1995). Studies on heat and cold tolerance in wild and obsolete wheat forms by Damania *et al.* (1993) revealed that *T. dicoccoides* was most susceptible to heat as well as cold. Among the diploids, *T. urartu* was significantly more cold tolerant than *T. boeoticum,* indicating perhaps the reason that the former can still be found at high altitudes in its center of diversity. Results of these studies are being used to identify the most suitable populations and sites and to develop a sustainable strategy, together with the appropriate land-management system, for *in situ* conservation of the indigenous wild wheat progenitors in Syria and the neighboring countries and adjoining territories.

With the initial support of the USDA, a project for *in situ* conservation of *T. dicoccoides* populations has been underway in Eastern Galilee in Israel for almost a decade. Between 1984 and 1989, individual plants were monitored at closely spaced permanent sampling points along with four topographically diverse transacts. Collections of single spikes were made annually from these plants and seed from progenies were sent for *ex situ* conservation. The 1-ha site is located 1 km west of Kibbutz Ammiad, in a hilly tract that is the southern extension of the Mt. Kenaan ridge. The *in situ* conservation site so established would protect and maintain the entire genepool of the selected populations. The climate is typical mediterranean with an average rainfall of 580 mm which falls during the winter months. As in Syria, the survival of these populations of wild wheat progenitors is now increasingly threatened by human population pressures and intensified mechanical agricultural practices of the settlers (Anikster and Noy-Meir 1991).

Some of the problems in areas of *in situ* conservation of wild species have been highlighted by results of the Ammiad experiments. One of the most difficult decisions of all in the establishment of such reserves is to determine the size of its area. The minimum viable population size will be greater than the minimum effective population size of individuals that can contribute to the next generation. During the last four years, the wild wheat study using the Ammiad methods of sampling and progeny testing has been extended to other wild populations, particularly in two nature reserves in Yahudiya, an area located in the Golan Heights, and Har Meiron in Upper Galilee (Anikster *et al.* 1997).

In situ conservation of wild wheat relatives at the Erebuni Nature Reserve, northeast of Yerevan in Armenia, has met with some success. Vavilov (1951) first recommended protection of this site because of its unique richness of the wider *Triticum* genepool. *Triticum urartu* was discovered there in 1935 by Tumanyan and later this species was fully described by Gandilyan (1972). Other wild wheat species, such as *T. boeoticum* and *T. araraticum,* grow in the protected area together with *Aegilops* spp. *Amblyopyrum muticum,* a species considered to be

taxonomically intermediate between *Aegilops* and *Agropyron,* was also found near this nature reserve. Hence, this site in Armenia is the only site outside Turkey where the uncommon species of the Anatolian highlands are found. The actual size of the reserve is about 100 ha but protection of a much wider area, about 400 ha, is needed in order to include rare populations of other species growing on the periphery of the protected area as well as to provide a buffer zone for the protection of the core area.

The need to encourage *in situ* conservation of landraces in the communities in which they occur has been advocated by several authors (Altieri and Merrick 1987; Brush 1995; Peña-Chocarro 1996). Qualset *et al.* (1997) caution that it is a challenge to undertake *in situ* conservation of indigenously developed germplasm without a return to or preservation of obsolete agricultural practices which may be unacceptable or impracticable under sociopolitical systems in areas where diversity abounds. Besides, conservation of germplasm of an economically important crop *in situ* would most probably also result in the conservation of associated species occurring naturally in the same ecosystem. *In situ* conservation also permits natural evolution to continue, an extremely important option for the preservation of genes for abiotic and biotic stress resistance as species coevolve with their pathogens and changing environment.

In situ methods of conservation of landraces and wild progenitors are, understandably, viewed skeptically by plant breeders. As long as genetic conservation and crop improvement are directly linked, any form of conservation will be judged by its short-term benefits to breeders, and *in situ* methods will attract considerable criticism (Brush 1991). On-site conservation is more plausible if these two goals are decoupled, making biodiversity conservation an end in its own right. In fact, Jana (1993) has said that we should get away from the notion that *in situ* conservation of biodiversity of wild progenitors and landraces is only for safeguarding breeding materials for the future. Conservation should be practised for its own sake; it keeps the landscape green, enhances the quality of life and ensures the continuation of the ecosystem, and thereby the wellbeing of humankind.

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Part 5. Historical Aspects and Crop Evolution

Genetic Evidence on the Origin of Triticum aestivum L. - J. Dvorák, M.-C. Luo and Z.-L. Yang

Introduction

Because of the great economic significance of wheat, its evolution has received a great deal of attention over the past 80 years. It was recognized early that wheat species fall into three natural groups according to their ploidy (Kihara 1924). Six biological species are recognized today, two at each ploidy level (Fig. 1). Of the six species, the most important economically is *Triticum aestivum* L., because it includes bread wheat. *Triticum aestivum* comprises a number of subspecies or other taxa which are interfertile and which differ from each other by a single or a few major genes (Mac Key 1966). In some of these subspecies, such as subsp. *aestivum* (bread wheat), subsp. *compactum* (Host) Thell. (club wheat), subsp. *sphaerococcum* (shot wheat) (Perc.) Mac Key, *T. petropavlovskyi* Udach. & Migush. (rice wheat) and subsp. *tibetanum* Shao (Tibetan wheat), glumes do not adhere to kernels and they are free-threshing. In contrast, subsp. *spelta* (L.) Thell. (spelt), subsp. *macha* (Dekapr. & Menabde) Mac Key, subsp. *vavilovii* (Jakubz.) A. Love and subsp. *yunnanense* King are hulled.

The fact that *T. aestivum* originated from hybridization of tetraploid *T. turgidum* L. (Fig. 1) with diploid *Aegilops tauschii* Coss. (Kihara 1944; McFadden and Sears 1946) is well documented by genetic evidence. Hexaploid wheat has been resynthesized by hybridization of *T. turgidum* with *Ae. tauschii* (McFadden and Sears 1946). The synthetic wheats resemble spelt and are invariably hulled (McFadden and Sears 1946; Kihara *et al.* 1965; Kerber and Rowland 1974). On the basis of this and other lines of evidence, it has been argued that spelt is ancestral to the free-threshing hexaploid wheat (McFadden and Sears 1946; Kuckuck 1959; Andrews 1964). Yet, some genetic and archaeological findings suggest that spelt may have been actually derived by introgressive hybridization between free-threshing *T. aestivum* and hulled *T. turgidum* subsp. *dicoccon* (Schrank.) Thell. (Tsunewaki 1968; Liu and Tsunewaki 1991; Nesbitt and Samuel 1996).

Whether the various forms of *T. aestivum* are monophyletic or polyphyletic is also open to debate. This uncertainty is true not only for subspecies but also for varieties within subspecies, such as the various types of spelt. Originally, spelt was known only from Europe which made it a poor candidate as an ancestral form of hexaploid wheat because *Ae. tauschii* does not grow anywhere nearby (Schiemann 1951). Later, spelt was discovered in Iran (Kuckuck and Schiemann 1957; Kuckuck 1959) and other locations in Asia. Jaaska (1978) concluded from isozyme variation in the A genome that the European spelt originated independently of the Asian spelt. The possibility that some of the subspecies and types of the Asian hulled wheats may be polyphyletic and may or may not be directly related to the evolution of free-threshing wheat must be seriously considered (Swaminathan 1966; Tsunewaki 1968; Johnson 1972).

A question related to the above dilemma is the exact source of the wheat D genome and the geographic place of the origin of *T. aestivum. Aegilops tauschii* encompasses several morphological varieties which are broadly grouped into two subspecies, *tauschii* and *strangulata* (Eig) Tzvelev. The former is distributed from eastern Turkey to China and Pakistan, whereas the latter occurs in two disjoined regions, southeastern Caspian Iran and Transcaucasia (Kihara *et al.* 1965; Jaaska 1995). Jaaska (1978, 1981) identified polymorphisms at the aspartate aminotransferase and aromatic alcohol dehydrogenase loci between the *Ae. tauschii* subspecies, and in both cases the subsp. *strangulata* allele corresponded to that in the *T. aestivum* D genome. *He* also pointed out that the profile of esterase alleles characterizing the D genome of *T. aestivum* fits subsp. *strangulata* better than subsp. *tauschii* (Jaaska 1980). The spectrum of alleles at the α-amylase loci in *T. aestivum* also corresponds better to the allele spectrum in subsp. *strangulata* than to that in subsp. *tauschii* (Nishikawa 1974; Nishikawa *et al.* 1980).

Fig. 1. Phylogeny of polyploid species of *Triticum* inferred from variation in repeated nucleotide sequences (Dvorák *et al.* 1988, 1993; Dvorák and Zhang 1990, 1992). Genomes of each species are indicated by capital letters.

Variation in the lengths of restriction fragments (RFLP) at a large number of single-copy loci and the rRNA gene

nontranscribed spacer at the *Nor3* locus was used to investigate genetic relationships among accessions of *Ae. tauschii* grouped according to their geographic origin and subspecies (Dvorák *et al.* 1998). Accessions from Turkey and western Iran were more closely related to those from Afghanistan, Turkmenistan and China than to those from the neighboring north-central Iran and southwestern Caspian Iran (Dvorák *et al.* 1998). A similar observation was made earlier by Lubbers *et al.* (1991). Dvorák *et al.* (1998) suggested that these findings reflect gene migration between subsp. *strangulata* and subsp. *tauschii* in Iran and proposed that *Ae. tauschii* is composed of two genepools, the *strangulata* and *tauschii* genepools, which do not correspond to the morphological delimitation of the subspecies. The *strangulata* genepool is wider than appears on the basis of morphology and comprises subsp. *tauschii* in north-central Iran and Caspian Iran. This study illustrated that morphology is of dubious value in assessing intraspecific genetic relationships.

In Transcaucasia, where the *strangulata* and *tauschii* genepools overlap (Jaaska 1995), genetic distances of individual accessions to subsp. *strangulata* and subsp. *tauschii* outgroups revealed that numerous accessions were allocated to an erroneous genepool on the basis of morphology (Dvorák *et al.* 1998). There is less introgression between subsp. *strangulata* and subsp. *tauschii* in Transcaucasia than in Iran. Only about 5% of all Transcaucasian accessions showed intermediate genetic distances to the outgroups; the rest of the accessions showed genetic relationships characteristic of either subsp. *strangulata* or subsp. *tauschii*. This contrasts with Caspian and north-central Iran where no accessions showing genetic relationships characteristic of true subsp. *tauschii* were found. Reallocation of Transcaucasian accessions to the respective genepools according to genetic relationships provided strong evidence that the *T. aestivum* D genome was contributed by the *strangulata* genepool (Dvorák *et al.* 1980).

Jaaska (1980) considered Transcaucasia to be the center of the distribution of subsp. *strangulata* and hence placed the origin of *T. aestivum* to Transcaucasia. Nishikawa *et al.* (1980) found that the α-amylase isozyme profile present in *T. aestivum* is most prevalent in southeastern Caspian Iran, not in Transcaucasia, and therefore suggested that the most likely birthplace of *T. aestivum* is southeastern Caspian Iran. Tsunewaki (1966) considered mountainous Azerbaijan as the place of the origin of *T. aestivum* because of the distribution of the waxy-bloom allele. Nakai (1979) placed the birthplace of *T. aestivum* in southwestern Caspian Iran and Transcaucasia on the basis of the distribution of esterase alleles.

In spite of the existence of polymorphism at isozyme loci in *Ae. tauschii*, no polymorphism has been found in the *T. aestivum* D genome that is shared with *Ae. tauschii*. Even at the highly polymorphic nontranscribed spacer at the *Nor3* locus encoding the 18S-5.8S-26S rRNA species (rDNA NTS), only a single *Ae. tauschii* allele has been detected in wheat (Clarke *et al.* 1989; Lagudah *et al.* 1991; Dvorák *et al.* 1998). The only potential exception to this may be the high-molecular-weight (HMW) glutenin locus *Glu1*. The locus is composed of two genes: *x*, encoding HMW-weight glutenin subunits with a slower electrophoretic mobility, and y, encoding HMW-weight glutenin subunits with a faster electrophoretic mobility. In the wheat D genome, the *Glu1a* haplotype encodes HMW-glutenin subunits 2 (*x* subunit) + 12 (*y* subunit). This haplotype has been detected in *Ae. tauschii* (Lagudah and Halloran 1988). Another, less common, haplotype in the wheat D genome is *Glu1d* which encodes subunits 5 (*x* subunit) + 10 (y subunit). A haplotype encoding similar subunits exists in *Ae. tauschii* (Lagudah and Halloran 1988). Two chromosomes ID carrying this haplotype have been substituted to *T. aestivum,* one from subsp. *strangulata* and one from subsp. *tauschii* (Jones *et al.* 1990, 1991). A close examination of the electrophoretic mobility of the subunits encoded by the *Ae. tauschii* haplotype revealed that the mobility of the HMW-glutein subunit 5 is identical in wheat and *Ae. tauschii.* The mobility of the wheat subunit 10 was found to be slightly slower under some electrophoretic conditions (Jones 1991). Lagudah and Halloran (1988) called this *Ae. tauschii* subunit 10 whereas Jones (1991) called it T5. Although Lagudah and Halloran (1988) could not distinguish the two forms of subunit 10 by electrophoretic mobility, they found that they differ in the isoelectric point. While the *Glu1* locus constitutes the only case in which more than a single *Ae. tauschii* allele at a locus may have been detected in wheat, because of the differences between subunits 10 and T5, the evidence is hardly conclusive, as pointed out by Lagudah and Halloran (1988).

The question of whether wheat originated by single or multiple hybridization events has ramifications for all of the problems discussed earlier. It is evident that if modern *T. aestivum* originated by multiple hybridization events, as speculated, e.g. by Jakubziner (1958), Dekaprelevich (1961), Kuckuck (1964), Morris and Sears (1967) and Yen *et al.* (1983), then the source of the *T. aestivum* D genome and the geographic place of its origin would be intrinsically uncertain. If wheat originated by a single hybridization event, as has been concluded by Jaaska (1980) or tacitly assumed by other authors (Liu and Tsunewaki 1991; Lubbers *et al.* 1991), all variation in the *T. aestivum* D genome would have originated since the origin of *T. aestivum,* which archaeologists place in the 7th millenium BC (for recent review, see Nesbitt and Samuel 1996). If, however, *T. aestivum* originated recurrently, some of the variation of *Ae. tauschii* would have been introgressed into wheat. These alternatives lead to different views of the wheat genetic system and wheat evolution.

To gain insight into these questions, polymorphisms of restriction fragment lengths (RFLP) at 53 single-copy loci, rDNA NTS and the HMW-glutenin locus *Glu1* were investigated with the objective of assessing parallel polymorphisms between *T. aestivum* and *Ae. tauschii* and the evolution of *T. aestivum.* Additionally, the electrophoretic mobility of HMW-glutenin subunits was investigated in *Ae. tauschii* and the *T. aestivum* D genome with the objective of determining whether the widespread D-genome haplotypes *Glu1a* and *Glu1d* were contributed by *Ae. tauschii.*

Material and methods

Plant material

RFLP was investigated in DNAs of 172 accessions of *Ae. tauschii,* 178 accessions of subsp. *aestivum,* subsp. *compactum* and Chinese endemic wheats (Tibetan wheat, Yunnan wheat and rice wheat), 64 accessions of spelt, 10 accessions of *T. aestivum* subsp. *macha* and 2 accessions of *T. aestivum* subsp. *vavilovii.* The spelt accessions consisted of 52 accessions

of the European spelt, 1 accession of spelt from Azerbaijan, 5 accessions of spelt from Iran, 2 accessions of spelt from Tadjikistan and 4 accessions of spelt from Afghanistan (the term spelt will be used only in reference to subsp. *spelta,* not to all hulled hexaploid wheats). The accessions and their sources have been described earlier (Dvorák *et al.* 1998). *Triticum aestivum* accessions were grouped according to subspecies and geographic region of origin (western and eastern). *Ae. tauschii* accessions were grouped by subspecies and the geographic region of the origin into 11 populations (Fig. 2).

RFLP

Nuclear DNA was isolated from leaves of a single plant per accession (Dvorák *et al.* 1988) and digested with DraI or XbaI. Restriction endonuclease-digestion, blotting, hybridization and DNA probes have been described previously (Dvorák *et al.* 1998). The position of each locus and allele in the wheat genomes was confirmed by synteny mapping using nullisomic-tetrasomic stocks (Sears 1966) and in some cases disomic substitution lines harboring single chromosome pairs of *Lophopyrum elongatum* (Host) A. Love substituted individually for wheat homoeologous chromosome pairs (Dvorák 1980; Dvorák and Chen 1984).

Variation at 55 loci was investigated (Dvorák *et al.* 1998). In *Ae. tauschii,* RFLPs at 53 loci were investigated in DraI-digested DNAs. For the *Nor3* locus, TaqI digests were employed, and for the *XGlu1* locus, XbaI digests were used. For 15 of the 53 single-copy loci, RFLP was also investigated in XbaI-digested DNAs. Thus, a total of 70 enzyme x probe combinations were used for *Ae. tauschii.* RFLP at the same 70 enzyme x probe combinations was also investigated in all accessions of *T. aestivum* subsp. *macha* and subsp. *vavilovii,* a limited sample of European and Asian *spelta,* and reference cv. Chinese Spring. Since some loci were monomorphic in *Ae. tauschii* or not informative in wheat, a subpopulation of 27 informative loci was selected for the investigation of the relationships between *Ae. tauschii* populations and those of *T. aestivum.* RFLP at 21 loci was investigated with DraI, two loci with XbaI, two loci with both DraI and XbaI, one locus with TaqI, and one locus with EcoRV. Thus, a total of 29 enzyme x probe combinations were used for the 27 loci.

Fig. 2. Approximate geographic location of *Ae. tauschii* populations used in this study: (1) Turkey, (2) Transcaucasia subsp. *strangulata,* (3) Transcaucasia subsp. *tauschii,* (4) western Iran, (5) southwestern Caspian Iran, (6) north-central Iran, (7) southeastern Caspian Iran subsp. *strangulata,* (8) southeastern Caspian Iran subsp. *tauschii,* (9) Turkmenistan, (10) Afghanistan and (11) China.

Shared polymorphism between *Ae. tauschii* and *T. aestivum*

Dvorák *et al.* (1998) reported polymorphisms in the *T. aestivum* D genome shared with *Ae. tauschii* at five loci. To scrutinize further the correspondence of these shared polymorphisms, several accessions of *Ae. tauschii* and *T. aestivum* representing each shared DraI or XbaI haplotype were selected and digested with either all or a subset of the following restriction endonucleases; ApaI, BglII, EcoRV, KpnI, SstI and XbaI. Southern blots were hybridized with clones detecting DNA fragments from these five loci. DNAs of relevant Chinese Spring nullisomic-tetrasomics and *L. elongatum* disomic substitution lines in the Chinese Spring genetic background were included in the blots. Restriction fragments belonging to the D-genome were identified in each restriction digest by comparing the profile of Chinese Spring with those of nulli-tetrasomics and disomic substitution lines.

HMW-glutenins

The endosperms of 222 accessions of *Ae. tauschii* and 25 accessions of *T. aestivum* were crushed, proteins were extracted and electrophoretically fractionated in denaturing polyacrylamide gels as described by Cole *et al.* (1981) and stained in 0.025% Coomassie brilliant blue R250 in 12% trichloracetic acid (TCA) for 24 hours and destained in 12% TCA for 2 days.

Results

Polymorphism sharing between wheat and *Ae. Tauschii*

Polymorphisms were encountered in the D genome of *T. aestivum* at 14 of the 70 enzyme x probe combinations representing 55 loci (Table 1). At five loci - *Xpsr899, Xpsr928, Xpsr666, Xpsr901* and *Glu1* - two Ae. *tauschii* haplotypes were found (Table 1). At 10 loci, haplotypes were found in *T. aestivum* which were not found in *Ae. tauschii;* a total of 18 haplotypes not encountered in *Ae. tauschii* were found in *T. aestivum* (Table 1). The possibility that some of these 18 *T. aestivum-specific* haplotypes are actually shared with *Ae. tauschii* but were not present among the *Ae. tauschii* accession investigated here cannot be discounted.

The *Xpsr899* locus was investigated with four restriction endonucleses. DNAs of *T. aestivum* and *Ae. tauschii* accessions having DraI haplotype *a* shared restriction fragments in all digests (Fig. 3). The same was true for accessions sharing haplotype *b* (Fig. 3). In all four digests, the fragments of the *a* haplotypes differed from those of the *b* haplotypes (Fig. 3), indicating that haplotype *a* differs from haplotype *b* in a number of restriction sites in both species. By these criteria, the *T. aestivum* haplotype *a* appears to be identical to haplotype *a* in *Ae. tauschii,* and *T. aestivum* haplotype *b* appears to be identical to haplotype *b* in *Ae. tauschii.*

The *Xpsr928* locus was investigated with six restriction endonucleases. Iranian and Azerbijan spelt and two accessions of Ae. *tauschii* represented the DraI haplotype *b* and Chinese Spring and two accessions of Ae. *tauschii* represented the DraI haplotype *a* (Fig. 4). Identical restriction fragments were shared by DNAs of the *T. aestivum* and *Ae. tauschii* accessions representing the DraI haplotype *b* in all six digests. However, DNAs of the *T. aestivum* and *Ae. tauschii* accessions

representing haplotype *a* shared the same fragments only in the KpnI and DraI digests (Fig. 4) suggesting that *T. aestivum* haplotype *a* is related but not identical to haplotype *a* in *Ae. tauschii* accessions KU2103 and KU2824. Actually, the two *Ae. tauschii* accessions also did not have identical haplotypes, as evidenced by polymorphism between them in the BglII and KpnI profiles (Fig. 4).

The *Xpsr666* locus was investigated with a total of seven restriction endonucleases. Chinese Spring and *Ae. tauschii* accessions KU2103 and KU2824 represented the XbaI haplotype *a* and Tadjikistan spelt VIR56569 and *Ae. tauschii* accessions KU2103 and KU2824 represented the XbaI haplotype *b*. No fragment belonging to the D genome was seen in the SstI digest and no polymorphism between haplotypes *a* and *b* was observed in the BglII and EcoRV digests. In the remaining four digests, haplotype *a* differed from haplotype *b* and the differences were the same in both species.

The *Xpsr901* locus was investigated with six restriction endonucleases. The D-genome restriction profiles in Chinese Spring and spelt PI367199 were identical to those in *Ae. tauschii* accessions KU2104 and KU2103 representing DraI haplotype *a* in all digests. The D-genome profiles in spelt PI90962 and PI347926 and *Ae. tauschii* accessions KU2112 and KU2151 representing DraI haplotype *b* shared the same DNA fragments in the DraI and SstI digests but not in the ApaI and BglII digests. In four digests - ApaI, BglII, DraI and SstI - *T. aestivum* *a* and *b* haplotypes differed/They were identical in the EcoRV and KpnI digests but the *Ae. tauschii* accessions representing haplotypes *a* and *b* differed. Because of the incomplete agreement between the DraI *b* haplotypes in wheat and *Ae. tauschii* accessions KU2112 and KU2151, all 85 *Ae. tauschii* having DraI haplotype *b* were digested with ApaI and BglII and Southern blots were hybridized with PSR901. Of the 85 *Ae. tauschii* accessions, only two, AL10/80-1 and AL10/80-2 collected in Nakhichewan by V. Jaaska (pers. comm.), had the same haplotype as spelt accessions PI90962 and PI347926. Both accessions belong to the *tauschii* genepool (Dvorák *et al.* 1998). Thus, there is a complete agreement between the DraI *a* haplotypes in *T. aestivum* and *Ae. tauschii* and between the DraI *b* haplotypes in *T. aestivum* and *Ae. tauschii* in all investigated restriction sites.

Table 1. Multiple allelisms in the D-genome of *T. aestivum* and the genome of *Ae. tauschii* and polymorphism sharing between *T. aestivum*[†] and *Ae. tauschii*[‡] in DNAs digested with DraI or a restriction endonuclease indicated in parentheses.

Groups of accessions	Xmwg2031	Xcdo 1400	Xpsr371-6D	XGlu1 (XbaI)	Xpsr899	Xbcd 1302	XEsi3	Xpsr666 (XbaI)	Xpsr102	Xpsr 901-2D	Xpsr 928	Xwg 644	XGsp	Xcdo 749
Ae. tauschii	a,b	b,c,d,e	a,b,c	<u>a</u>,<u>b</u>,c,d	<u>a</u>,b,c,d,e,<u>f</u>,g	b,c,d,e,f	b,c,d	<u>a</u>,<u>b</u>,c	a,b	<u>a</u>,<u>b</u>	<u>a</u>,<u>b</u>	a,b,c	b,c,e,f	a,b,c,d
wheat west reg.	a	**a**,c	a	a,b	a,f,**h**,**i**	**a**,**g**	d	a	a,**c**	a,b	a,b	a	**a**	a
wheat east reg.	a	**a**,c	a,**d**,**e**	-	a,f	**a**,c	**a**,d	a,b	a,**d**	a,b	a,b	a	**a**	a
subsp. *macha*	a	c	a	a,b	a,f,**j**,**k**	**a**	**a**,d	a,d	a,**d**	a,b	a,b	a	**a**	a,**e**
spelt (Asia)	a,**c**	c	a	a	a,f	**a**,c	d	a,b	a,**d**	a	a,b	a	**a**	a
spelt (Europe)	a	c,**f**	a	a	a,f	**a**	d	a	a,**c**,**d**	a,b	a	a,**b**	**a**	a
subsp. *vavilovii*	a	c	a	a	a,f	**a**	**a**,d	a	d	a	a	a	**a**	a

[†] *T. aestivum* haplotypes which were not found in *Ae. tauschii* are in bold.

[‡] Pairs of *Ae. tauschii* haplotypes shared with *T. aestivum* are underlined.

Fig. 3. Autoradiograms of Southern blots of DNAs of *Ae. tauschii* and *T. aestivum* accessions and Chinese Spring cytogenetic stocks digested with BglII (left) and DraI (right) restriction endonucleases and hybridized with pPSR899. Accessions sharing haplotype a and those sharing haplotype *b* are indicated at the bottom. Genome allocation of major bands is indicated. Note the absence of the Chinese Spring fragments assigned to chromosome 2D in the disomic substitution line 6E(6D). Note that the D-genome DNA fragments of the *Ae. tauschii* and *T. aestivum* accessions with haplotype *a* differ from those shared by *Ae. tauschii* and *T. aestivum* accessions with haplotype *b* in both digests.

The *Glu1* locus was investigated with five restriction endonucleases. *Triticum aestivum* was polymorphic in the XbaI and EcoRV digests. The same DNA fragments were observed in *Ae. tauschii* (Table 1). In *Ae. tauschii,* the XbaI haplotypes *a* and *b* had frequencies 0.21 and 0.07, respectively, and the EcoRV haplotypes *a* and *b* had frequencies 0.94 and 0.06, respectively (not shown) indicating that the *b* haplotype is rare in *Ae. tauschii.* Of 172 *Ae. tauschii* accessions, XbaI haplotype *b* was found in 12 accessions and EcoRV haplotype *b* was found in 10 accessions (Table 2). Of these, eight shared the two haplotypes, indicating that the XbaI and EcoRV *b* haplotypes are in a strong linkage disequilibrium in *Ae. tauschii.*

Fig.4. Autoradiograms of Southern blots of DNAs of *Ae. tauschii* and *T. aestivum* accessions and Chinese Spring cytogenetic stocks digested with DraI (left) and KpnI (right) restriction endonucleases and hybridized with pPSR928. Accessions sharing haplotype *a* and those sharing haplotype *b* are indicated at the bottom. Genome allocation of major bands is indicated. Note the absence of the Chinese Spring fragments assigned to

Seven types of the *x* subunit of HMW-glutenin and eight types of the *y* subunit were found with SDS-PAGE (not shown). Most of the *Ae. tauschii* accessions with the DNA haplotype *b* had the HMW-glutenin x subunit 5 (Table 2, Fig. 5). The haplotype encoding subunit 5 was found to be rare in Ae. *tauschii,* frequency (*f*) = 0.06 (Table 3).

None of the accessions with the b DNA haplotype had the *x* subunit 2 or any other *x*-type subunit frequent in *Ae. tauschii.* Thus, the XbaI and EcoRV haplotypes *b* and the *Glu1x* allele encoding subunit 5 usually occur together and must be in a strong linkage disequilibrium in *Ae. tauschii.*

The same linkage disequilibrium exists in *T. aestivum.* Seed storage proteins were extracted from seeds of 25 accessions of the Asian and European spelt, subsp. *macha,* subsp. *vavilovii* and bread wheat cultivars of both western and eastern origin and fractionated by SDS-PAGE. Eight accessions had HMW-glutenin subunits 5 + 10 (haplotype *Glu1d*) and 17 had HMW-glutenin subunits 2 + 12 (haplotype *Glu1a*). All *Glu1d* accessions had EcoRV haplotype *b* and all *Glu1a* had EcoRV haplotype *a* (XbaI digests were not investigated because it was difficult to score the XbaI fragment in the wheat genetic background). These parallels between the *T. aestivum* D genome and *Ae. tauschii* showed that *T. aestivum Glu1a* and *Glu1d* haplotypes encoding HMW-glutenin subunits 2 + 12 and 5 + 10, respectively, were both contributed to *T. aestivum* by *Ae. tauschii.*

In *Ae. tauschii,* the *Glu1a* haplotype encoding HMW-glutenin subunits 2 + 12 occurs in Transcaucasia, the southeastern Caspian region and north-central Iran. The *Glu1a* haplotype was observed only in the *strangulata* genepool (Table 3). The haplotype encoding the pair of subunits 5 + T5, which corresponds to the wheat haplotype *Glu1d* (Fig. 5), was also observed only in the *strangulata* genepool; its highest frequency was in southwestern Caspian Iran (Table 3). Likewise, the *x* gene encoding subunit 5 occurred in the highest frequency in southwestern Caspian Iran (Table 3).

Discussion

Multiple contributions of *Ae. tauschii* to the wheat D genome

Pairs of haplotypes shared by *Ae. tauschii* and the *T. aestivum* D genome were found at five of the 55 investigated loci. Within each pair, haplotypes differed in multiple restriction sites. If these were merely restriction site differences or small independent insertions or deletions, it would be extremely unlikely that these parallel polymorphisms originated by reverse mutations in wheat. Several reverse mutations would have to occur in each case to convert one haplotype into the other, which is very unlikely. If, however, each of the polymorphisms is due to a single large DNA insertion that occurred in *Ae. tauschii,* an excision of the inserted DNA during wheat evolution could convert a haplotype into the ancestral one and, thus, generate a shared haplotype pair between wheat and *Ae. tauschii.*

This scenario can be discounted for the shared polymorphism at the *Glu1* locus because the *Glu1a* and *Glu1d* haplotypes differ by several independent mutations. Should the difference between the wheat *Glu1a* and *Glu1d* haplotypes be due to reverse mutations, a minimum of three independent reverse mutations, HMW-glutenin subunit 5 to 2 (or vice versa), HMW-glutenin subunit 10 to 12 (or vice versa) and EcoRV haplotype *b* to *a* (or vice versa) would have to have occurred during wheat evolution. This is extremely unlikely.

Three of the five loci in which polymorphisms are shared between *T. aestivum* and *Ae. tauschii* are linked on chromosome 2D. Two, *Xpsr666 and Xpsr928,* are on the short arm and one, *Xpsr901,* is closely linked to them on the long arm (for map positions of these loci see Dubcovsky *et al.* 1996). Linkage among the polymorphic loci would hardly be expected if the polymorphisms were caused by reverse mutations, since these should be random. An intriguing coincidence is that chromosome 2D played a critical role in the evolution of the free-threshing *T. aestivum.* The free-threshing character is based on two mutations, the dominant mutation of *q* to Q on the long arm of chromosome 5A, and a recessive mutation of *Tg* to *tg* at the end of the short arm of chromosome 2D (Kerber and Rowland 1974). Chromosome 2D was substituted from four accessions of *Ae. tauschii* into bread wheat cv. Chinese Spring, which is *QQtgtg*. All four disomic substitution lines had adhering glumes in spite of having Q allele (J. Dvorák, unpublished). Clearly, Q itself is insufficient to cause a free-threshing habit. Therefore, the evolution of the free-threshing habit required fixation of a recessive *tg* mutation in *T. aestivum.* One can imagine a scenario in which a *Tg* to *tg* mutation happened more than once. Selection for the *tg* alleles could maintain hitchhiking linked polymorphisms on chromosome 2D in the wheat genepool.

Table 2. Lists of *Ae. tauschii* accessions (out of 172 investigated) having the rare XbaI and EcoRV haplotypes *b* at the *Glu1* locus and the HMW-glutenin subunits encoded at the *Glu1* locus in these accessions.

XbaI	EcoRV	HMW-glutenin subunits
KU20-10	KU20-10	5 + T5
KU2104	KU2104	5 + 12
KU2090	KU2090	5 + T5
	KU2106	5 + null
KU2160	KU2160	5 + T5

KU2110	KU2110	5 + 12
	KU2001	3 + 12
AL8/78-2	AL8/78-2	T6 + T8
AL9/78-3, -4, -6, -7		T6 + T5
AL10/80-1, -2	AL10/80-1, -2	5 + T9

Fig. 5. SDS-PAGE profiles in indicated *Ae. tauschii* accessions (KU), disomic substitution line in which the Cheyenne 1D chromosome was substituted for 1D of Chinese Spring (DSCnn1D), and Chinese Spring (CS). Subunits encoded by *Glu1* haplotypes are indicated in parentheses. The *x* HMW-glutenin subunits (2 and 5) and y HMW-glutenin subunits (10, T5, and 12) are indicated by arrowheads. Chinese Spring profile shows subunits 2 + 12 (haplotype Glu1a), the profile of DSCnn1D shows subunits 5 + 10 (haplotype *Glu1d*), the profile of *Ae. tauschii* accessions KU2122 shows subunits 5 + T5, the profile of *Ae. tauschii* KU2121 shows subunits 2 + T5, and that of *Ae. tauschii* KU2110 shows subunits 5 + 12. Note that the mobility of subunit 5 in wheat and *Ae. tauschii* is identical. Likewise the mobility of subunits 10 and T5 is indistinguishable from each other in this gel.

Fig. 6. Phenograms produced by the neighbor-joining method using genetic distances based on 55 loci (top) and selected 27 loci (bottom). The magnitude of divergence between groups was computed as Nei's genetic distance *D* (Nei 1978) with the GDA program (Lewis and Zaykin 1997). The phenograms were constructed with the GDA program. A scale showing a Nei's genetic distance is shown. The phenogram based on 27 loci is longer than that based on 55 loci because it involves only highly informative loci (from Dvorák *et al.* 1998). In each phenogram, T = subsp. *tauschii* and S = subsp. *strangulata.*

Table 3. Frequencies of haplotypes encoding the indicated pairs of HMW-glutenin subunits in *Ae. tauschii* accessions grouped by geographic region and botanical subspecies (the frequencies were zero in the remaining regions).

Geographic region	Subspecies	2 + 12	5 + T5	5 + any subunit
Transcaucasia	*tauschii*	0.00	0.10	0.10
Transcaucasia	*strangulata*	0.29	0.00	0.03
Southwest Caspian Iran	*tauschii*	0.00	0.14	0.36
Southeast Caspian Iran	*tauschii*	0.00	0.00	0.00
Southeast Caspian Iran	*strangulata*	0.33	0.04	0.10
North-central Iran	*tauschii*	0.33	0.00	0.00

Sources of the wheat D genome and the geographic origin of *T. Aestivum*

Most of the evidence accumulated thus far suggests that the *Triticum aestivum* D genome is more related to the *strangulata* genepool than to the *tauschii* genepool (Nishikawa 1974; Jaaska 1978, 1980, 1981; Nakai 1979; Nishikawa *et al.* 1980; Lagudah *et al.* 1991, Dvorák *et al.* 1998). On a geographic region basis, the D genomes of all forms of *T. aestivum* were found to be most closely related to accessions of the *strangulata* genepool collected in Transcaucasia and southwestern Caspian Iran (Dvorák *et al.* 1998; see Figure 6). On the morphological basis, the former accessions belong to subsp. *strangulata* but the latter, collected by Kihara *et al.* (1965) in the coastal southwestern Caspian Iran, belong to subsp. *tauschii.* The latter population is composed of morphological varieties *meyeri* and *typica* (Kihara *et al.* 1965). On the genetic basis, however, there is no appreciable genetic distinction between the two varieties in this region and both belong to the *strangulata* genepool (Dvorák *et al.* 1998). Therefore, characteristics attributed to var. *meyeri* are pertinent to the entire southwestern Caspian population. Lagudah *et al.* (1991) failed to find the *Nor3a* restriction pattern, for which wheat is monomorphic (Clarke *et al.* 1989; Lagudah *et al.* 1991; Dvorák *et al.* 1998), and the *Glu1a* haplotype in var. *meyeri*. While the *Nor3a* restriction pattern does occur, and in a high frequency, in southwestern Caspian Iran (Dvorák *et al.* 1998), the *Glu1a* haplotype was indeed not found in that region (present data). The *Glu1a* haplotype is present in the Transcaucasian and southeastern Caspian subsp. *strangulata.* The *Glu1x* gene encoding the HMW-glutenin subunit 5 occurs with a high frequency in Transcaucasia and southwestern Caspian Iran and the *Glu1* haplotype encoding HMW-glutenin subunits 5 + T5, which is ancestral to wheat haplotype *Glu1d,* occurs with the highest frequency in southwestern Caspian Iran. Thus, variation at the *Nor3* and *Glu1* loci is consistent with inferences based on genetic distances (Dvorák *et al.* 1998) indicating that the *strangulata* genepool in Trancaucasia and southwestern Caspian is the most likely source of the *T. aestivum* D genome. Earlier, Tsunewaki (1966) and Nakai (1979) placed the origin of *T. aestivum* to southwestern Caspian Iran and the neighboring mountainous Azerbaijan on the basis of the distribution of the waxy bloom and esterase alleles and Jaaska (1981) to Transcaucasia on the basis of the distribution of aspartate aminotranferese and aromatic alcohol dehydrogenase alleles.

To investigate individual regions of Transcaucasia, Transcaucasian accessions were divided into four geographic regions: Georgia, Armenia, Nakhitshevan and Azerbaijan (Dvorák *et al.* 1998). The D genome of *T. aestivum* appeared to be most closely related to the *strangulata* genepool in Armenia (Dvorák *et al.* 1998). Most of the Armenian accessions were collected in the vicinity of Jerevan and along the Razdan River (Kihara *et al.* 1965; V. Jaaska, pers. comm.). Although genetic distances point to Armenia, other areas in Transcaucasia and potentially western coastal Caspian Iran may have played a role in the evolution of the *T. aestivum* D genome as well (Dvorák *et al.* 1998). First, differences among genetic distances between wheat and *strangulata* genepool accessions grouped by geographic regions in Transcaucasia and

southwestern Caspian Iran are not large. Second, it was shown here that multiple *Ae. tauschii* sources contributed to the evolution of the *T. aestivum* D genome. There is no reason to suppose that these multiple *Ae. tauschii* sources were from a single geographic area or, in fact, that they all were from only the *strangulata* genepool. One of the five loci at which wheat and *Ae. tauschii* share polymorphism is the *Xpsr901* locus. Only two of the 172 investigated *Ae. tauschii* accessions matched the restriction sites of the *T. aestivum* haplotype *b*. Both came from a single population from Nakhichean and both belonged to the *tauschii* genepool. Third, it is not known to what extent the distribution and genetic structure of the present-day populations of *Ae. tauschii* were affected by agriculture, particularly the cultivation of wheat in Transcaucasia and the nearby Iranian regions.

Genetic distances calculated from RFLP in the D genome suggest a very close relationship of both western and eastern accessions of bread wheat with the Asian spelt (Dvorák *et al.* 1998). These distances are about a tenth of the genetic distances between bread wheat and the European spelt (Dvorák *et al.* 1998). This finding agrees with Jaaska's (1978) conclusion that the European spelt differs from the Asian spelt. The D genome of the European spelt appears, in turn, more related to bread wheat than is that of subsp. *macha* and subsp. *vavilovii* (Dvorák *et al.* 1998). Although these findings could be interpreted to mean that bread wheat evolved from the Asian spelt, they could be equally well interpreted to mean that the Asian spelt was derived recently from bread wheat by mutation or hybridization of free-threshing bread wheat with hulled tetraploid wheats (see Introduction). Additional work is therefore needed to resolve this dilemma. However, monophylesis of all *T. aestivum* groups in the dendogram based on variation in the D genome (Fig. 6) and the observation that many polymorphisms unique to *T. aestivum* are shared among the various forms of *T. aestivum* (Table 1) strongly suggests that all forms of *T. aestivum* likely have evolved from a common hexaploid genepool (Dvorák *et al.* 1998).

Agriculture appears in Transcaucasia in the 6th millenium (Mellaart 1975). Findings of free-threshing hexaploid wheat in archaeological sites in Anatolia between 6000 and 7000 BC (Hillman 1978; de Moulins 1993) require rapid evolution of hexaploid wheat upon the arrival of wheat cultivation to Transcaucasia. If this timetable is correct, the antiquity of this hexaploid genepool would conceptually provide sufficient time for the evolution of modern free-threshing and hulled forms of *T. aestivum* by mutation or hybridization from this ancient genepool.

There are two basic scenarios by which the D-genome genepool could have been formed. Several amphiploids could have originated and their hybridization and recombination could have led to the evolution of a single genepool. Alternatively, a single amphiploid could have originated and founded a hexaploid population. Plants in this hexaploid population could have hybridized with *Ae. tauschii* and the hybrids could have been a bridge for geneflow from *Ae. tauschii* to *T. aestivum.* This scenario seems unlikely. While hybridization between tetraploid wheat and *Ae. tauschii* is easy and fertile amphiploids are produced by self-pollination of triploid hybrids owing to high production of unreduced gametes (Kihara *et al.* 1950), hybridization between hexaploid wheat and *Ae. tauschii* is difficult and production of hybrid plants usually requires embryo rescue. Therefore, the recurrent appearance of hexaploid amphiploids in the fields of tetraploid wheat or mixed tetraploid/hexaploid wheat was a likely source of geneflow from *Ae. tauschii* to the hexaploid genepool.

If multiple amphiploids contributed to the formation of the genepool ancestral to all present-day forms of *T. aestivum,* it is puzzling why shared polymorphisms between *T. aestivum* and *Ae. tauschii* are rare. An obvious example is rRNA gene locus *Nor3* which is highly polymorphic in *Ae. tauschii* but appears to be monomorphic in *T. aestivum* (Lagudah *et al.* 1991; Dvorák *et al.* 1998). Since the *Nor3a* haplotype is rare in *Ae. tauschii* it is unlikely that this haplotype was present in every amphiploid that was involved in the formation of *T. aestivum.* This contradiction can be accounted for if it is assumed that the D-genome genepool was subjected to significant evolution prior to the differentiation of the modern forms of *T. aestivum.* The dates of the appearance of free-threshing wheat in archaeological sites provide ample time for this phase of *T. aestivum* evolution. During this phase, some polymorphic loci may have become monomorphic. Once the hexaploid genepool became large, most alleles contributed to the genepool by subsequent amphiploids would have a general tendency to be lost, unless they were selected for or hitchhiked with selected alleles. New amphiploids would be particularly disadvantaged in the fields of free-threshing wheat because their adhering glumes would tend to eliminate them during threshing.

Acknowledgments

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Introgression of Durum into Wild Emmer and the Agricultural Origin Question - M.A. Blumler

Introduction

The transition from hunting/gathering to farming was a crucial watershed in human history, with enormous ramifications continuing right down to the present day (Diamond 1997a, 1997b). In recent decades, a highly productive burst of archaeological investigations into the origins of agriculture, complemented by equally fruitful cytogenetic studies of crop phylogeny, has shed considerable light on this crucial time period. Nonetheless, our understanding of the reasons for the transition to agriculture remains limited, and subject to legitimate debate (Blumler and Byrne 1991). A major problem is that archaeologists have found it extremely difficult to locate sites that display the transition from the use of wild plants and animals to the raising of domesticated species (Blumler 1992a). Most sites show hunting/gathering only, farming only, or hunting/gathering followed abruptly by an agricultural economy that is clearly at least in part intrusive from elsewhere (e.g. Hillman *et al.* 1989). For instance, Pickersgill and Heiser (1977:829) pointed out that the famous site of Tehuacan, Mexico, displays "domesticates but not domestication." That is, domesticated crops apparently filtered into Tehuacan from some other place, where their wild progenitors previously had been taken under cultivation and domesticated. This is true not only of Tehuacan, but of all or almost all other archaeological sites as well (Smith's 1997 re-analysis of the Oaxacan squash remains may be an exception). Thus, we have a great deal of information about the spread of agriculture, but not about its inception. Until archaeologists locate the sites where domestication actually occurred, where hunter-gatherers made the decision to farm, independently (i.e. free from the influence of already existing farmers), it will be difficult to move beyond speculation concerning causes.

This difficulty was largely unanticipated, because archaeologists (and a few influential crop geneticists) had assumed that most crops were domesticated independently many times by many different small human populations. Consequently, it should not be so difficult to locate a site showing the complete transition from wild to domesticated organism. For instance, Harlan (1975) asserted that emmer wheat (*Triticum dicoccum*) no doubt was domesticated many times in various parts of the Fertile Crescent. This assumption rested upon a theoretical stance that Harlan, and most others concerned with agricultural origins, adopted in the 1950s in the context of a highly polarized debate over the importance of diffusion (the people on the 'other side' in this debate were geographers, notably Carl Sauer). It is obvious from Harlan's writings on the subject that this was one of those debates that generated far more heat than light, with scurrilous charges of racism being bandied about in attempts to discredit opposing viewpoints. Sadly, as often happens in such circumstances, scholars became locked into extreme and inflexible viewpoints (Blumler 1993, 1996). Only recently, as a profusion of new, cytogenetic and distributional evidence concerning the wild progenitors of crop species has become available, has it become possible to re-examine the issue dispassionately (Zohary 1989; Blumler 1992a). This new evidence demonstrates very clearly that, in most regions where agriculture began, primary crops were domesticated only once or a very few times (Table 1). Moreover, while Sauer's (1952) specific hypothesis concerning agricultural origins is probably invalid, his underlying premise that diffusion is far more important than independent invention is undeniably correct (Blumler 1996).

On the one hand, that so many primary crops were domesticated only once or twice makes the archaeologist's search for the agricultural transition analogous to attempting to find a needle in a haystack. On the other hand, it also means that it should be possible to narrow down the location of domestication by cytogenetic analysis, whereupon archaeological exploration might become more successful. With a single origin, only a small subset of the wild genepool is involved in domestication. If the progenitor genotype(s) is geographically restricted, as is often the case, a plausible center of origin can be delineated. For instance, Gepts (1990, this volume) has concluded that the common bean (*Phaseolus vulgaris*) was domesticated in Jalisco, Mexico and in northwestern Argentina. Since several additional crops also seem to have arisen in these two geographical areas, archaeological exploration is clearly called for (Blumler 1992a). Similarly, Heun *et al.* (1997) identified forms of wild einkorn (*T. boeoticum*) from Mt. Karacadag in southeastern Turkey as the nearest genetic relatives of einkorn (*Triticum monococcum*). Several archaeological sites in the vicinity of Karacadag provide evidence that einkorn was a very early domesticate there.

While this approach is promising, several limitations need to be kept in mind: (1) it assumes that the important ancestral genotypes are still extant, (2) it assumes no change in wild genotype distribution in the 10,000 years since domestication, despite considerable evidence for dramatic climatic changes during this time period, and (3) introgression from cultivars can cloud the picture. I focus on the latter problem in this paper. In brief, the difficulty is that presumed 'wild' individuals may be genetically similar to the domesticate because of geneflow from the crop into wild populations, and hence be mistaken for the progenitor. Therefore, it is important to recognize introgression where it occurs, and to determine what the genetic composition of the introgressed individuals would have been before they received genes from the domesticate, prior to carrying out the phylogenetic analysis (Blumler 1994).

Table 1. Most likely number of domestication events for putative primary crops and animals (Blumler 1992a, 1996), illustrating that most species apparently were domesticated only once in any given hearth region.

Domesticate	Most likely number of domestications
Near East	
Emmer	1
Einkorn	1
Barley	2

Pea	1
Lentil	1
Chickpea	1
Broad bean	1
Bitter vetch	2
Flax	1
Sheep	1
Africa	
Finger millet	1
Pearl millet	1
Yam bean	2
Andes	
Common bean	>3
Potato	1
Mexico	
Maize	1
Common bean	1
Tepary bean	1
Scarlet runner	2
Peppers	1
Amaranths	1
Squash (*Cucurbita pepo*)	2†
Other	
Sunflower	1
Rice	2
Sweet potato	1
Chicken	1
Cattle	2
Dog	2

† Includes possible eastern US domestication event.

In practice this is difficult to do, although the best cytogenetic investigations into crop origins, such as the two mentioned above, have attempted to deal with the issue. Gepts (1990) and Gepts *et al.* (1986) accepted the criteria laid down by the International Center for Tropical Agriculture (CIAT) for identifying possibly introgressed individuals of wild common bean, and discounted such individuals. Heun *et al.* (1997) also devised a small set of morphological indicators of introgression in wild einkorn, and showed that the Karacadag populations do not possess these indicators. The problem, however, is that the criteria for identifying introgressed individuals are somewhat open to question. Some traits, such as lack of a seed-dispersal mechanism, seem clearly maladaptive in the wild but adaptive in the cultivated field, and consequently can be taken as likely indicators of introgression (Harlan *et al.* 1973; Blumler and Byrne 1991). On the other hand, populations sometimes are assumed to be introgressed merely because they tend to grow in and around cultivated fields (so-called 'weedy' forms), or because they produce large seeds, another common domesticated trait. But weedy tendencies or the ability to manufacture large seeds do not necessarily mean that introgression has occurred. 'Weedy' plants may be adapted to fertile soil conditions, and such genotypes may have been those initially cultivated by incipient agriculturalists. Similarly, the first farmers may have cultivated large-seeded genotypes of the ancestral wild species. Certainly, they tended to domesticate large-seeded species (Blumler 1992b, 1994; Diamond 1997a). In fact, Harlan and Zohary (1966) suggested that a large-seeded race of wild emmer wheat (*T. dicoccoides*), from the vicinity of the Upper Jordan Valley, is the likely progenitor of cultivated emmer and its successors, durum (*T. durum*) and bread wheat (*T. aestivum*), because of the wild race's similarity to domesticates in seed size and other morphological characters. In short, an improved ability to discriminate introgressed from truly wild individuals should foster a fine-tuning of the phylogenetic analysis of crop origins, and increase confidence in the results. I use the example of wild emmer below to illustrate some of the complexities involved, and to point the way toward such fine-tuning.

Wild emmer wheat

Wild emmer, a tetraploid, is the ancestor of most wheat cultivated today. It is distributed in the Fertile Crescent, from Palestine and Jordan to southeastern Turkey, northern Iraq and western Iran. It is more common in the western portion of this arc, while another, morphologically almost identical, wild tetraploid species (*Triticum araraticum*) is common in the eastern portion. When Harlan and Zohary (1966) proposed that emmer had been domesticated in or near the Upper

Jordan Valley, it was not yet recognized that *T. dicoccoides* occurs in the eastern and northern portions of the Fertile Crescent. This fact became known in time for Zohary (1969) to modify his position, though in a note added in proof to his paper. Although the paper is widely read, many archaeologists have perhaps (understandably) overlooked the key footnote in which he pointed out that the species may have been domesticated almost anywhere in the Fertile Crescent, and not necessarily in the Upper Jordan Valley. Consequently, there appears to be some confusion about the geneticists' conclusions, with some scholars interested in agricultural origins continuing to believe that the Upper Jordan Valley has been identified as the most likely locus of domestication.

Indeed, many wild individuals from this region do look a lot like domesticated wheat. Especially in that portion of the valley just north of the Sea of Galilee, plants resemble domesticates in being robust, large-seeded, early maturing, and also in such specific traits as lack of anthocyanin pigment. Moreover, electrophoretic studies demonstrate that the wild emmer populations in this sector of the valley are sharply differentiated genetically from all other investigated Palestinian populations, so much so that a case could be made for classifying these populations as a separate species (Nevo *et al.* 1982; Golenberg 1986); here, it is categorized as the Upper Jordan Valley (UJV) race of wild emmer. This race disappears rapidly as one travels from UJV to the east or west, and is replaced by populations that are similar in their electrophoretic alleles to other Palestinian populations (Golenberg 1989; Blumler 1994).

In UJV, wild emmer is reported to be extremely abundant, especially where grazing is light, suggesting that it is well adapted to truly wild conditions (Zohary 1969; Noy-Meir 1990). Moreover, wild emmer is known to be scarcely if ever weedy (Harlan and Zohary 1966; Blumler and Byrne 1991), and is reported to have only limited geneflow (Golenberg 1987), so that introgression would seem to be less likely than in other crop progenitors that are common in cultivated fields. On the other hand, hybrid swarms (including one of several thousand individuals) were securely identified in UJV, on the edge of formerly cultivated fields (Zohary and Brick 1961). Little wheat is grown in UJV today, but formerly the region was long a center of durum production. For instance, the Biblical parable of the loaves and fishes is situated in UJV. More recently, up until 1948, there were many Palestinian villages in UJV, the denizens of which would have cultivated durum. Most of the Palestinian villages were destroyed during the 1948 war although a Bedouin settlement was left intact (Falah 1996). The continuing existence of this village, with its emphasis on pastoralism, seems to have given some scholars the false impression that traditional land use in UJV was pastoral when in fact farming played a major role. Thus, domesticated individuals should have had opportunities to come in contact with wild plants, especially along rocky, untillable field margins. Scholarly opinion concerning the resulting frequency of hybridization varies greatly, with some believing that there has been essentially no introgression, and others asserting that there was a great deal.

Harlan and Zohary were not the first to propose Palestine as the place where wheat farming began. N.I. Vavilov traveled through the region in 1926; he noticed "a peculiar subspecies of wild wheat [that] accompanies cultivated hard wheat in Palestine" (Vavilov 1957:98), and concluded that it must be the wild progenitor because of its similarity to the domesticate. So distinct from other forms of wild emmer that he classified it as a subspecies, his description fits UJV. Yet he encountered his new subspecies to the south, at the edge of the Esdraelon Plain:

> "At the base of the hills, from which flows the underground River Esdraelon, we observed large growths of wild wheat in mixture with wild double-rowed barley. This was an abandoned lot with soft fertile ground positioned right next to the field. The wheat here had a very different appearance from that which we collected in Hauran, Syria. Spikes were large, but with rough spikelets and large seeds. This was no longer an extreme of a xerophyte, but essentially a plant close to cultivated wheat.

> "Investigating the fields of the Esdraelon Valley, we found wild wheat in large quantities on edges, along boundaries. No doubt it represents the closest wild source of cultivated wheat, especially hard wheat." (Vavilov 1962:141)

Subsequent Russian taxonomists have maintained Vavilov's bipartite division of the species into a large-seeded Palestinian subspecies *judaicum,* and a small-seeded subspecies *horanum,* though their descriptions of *judaicum* are not entirely concordant (Jakubziner 1932; Poyarkova 1988). Jakubziner reported that *judaicum* occurs primarily in the Esdraelon but also is found in UJV, Mt. Hermon, Syria, Jordan and even in the Cilician Taurus. He also described some hybrids that had been collected in UJV. In addition, he noted that *judaicum* populations usually include some *horanum* individuals. Finally, both Jakubziner (1932) and Vavilov (1962) were struck by the great variability of *judaicum* in contrast to the ubiquitous *horanum.*

These observations, taken together, suggest introgression. The Esdraelon is a region that supported extensive durum cultivation in Vavilov's time, but today is given over to other crops. It appears that Esdraelon populations of wild emmer were located at the base of rocky, untillable slopes, at the edges of deep soil and cultivation -precisely where hybridization between a crop and a non-weedy species would be most likely to occur. One expected outcome of introgression would be high variability. Another would be possible reduction or elimination of the stands after cultivation ceased. Israeli geneticists have collected wild emmer intensively throughout their territory, but have never reported populations from the Esdraelon. Other *judaicum* specimens discussed by Jakubziner also seem to be from areas of intensive cultivation. For instance, he describes *judaicum* from Mt. Hermon, at Majdal es-Shams, a population center in a wheat-growing region.

Approaches to the identification of introgression

Several lines of investigation are proving fruitful in identifying introgression in wild emmer, and should be useful in other species as well (Box 1). First, while introgressed individuals should resemble domesticates, they should be more similar to

modern varieties than to primitive ones. Progenitors, on the other hand, should resemble primitive forms of the domesticate more than later-evolving derivatives. For example, wild emmer gave rise initially to emmer, which is rarely cultivated today, and not at all in Palestine. Emmer later evolved into durum and several other tetraploid wheats, while bread wheat is an allopolyploid derivative. In recent centuries, durum has been the major wheat cultivated in Palestine, though there has been a shift toward more bread wheat since 1948. Introgression from the latter would be limited because of the difference in ploidy level, though it does occur (Dorofeev 1969). Thus, one would predict that UJV plants will resemble durum more than emmer if introgressed, while they will be more similar to emmer if they represent the genotypes originally taken under cultivation.

Second, the ecological conditions to which wild plants must adapt are very different from those which a domesticate faces, and this results in varying degrees of selection for morphological and other characteristics. For instance, indehiscence is strongly selected against in the wild, since the seed needs to disperse from the top of the plant and find its way to the soil in order to germinate. In contrast, indehiscence is usually selected under cultivation (Harlan *et al.* 1973; Blumler and Byrne 1991). The presence of indehiscent individuals in wild populations, therefore, suggests very recent introgression. Similarly, domesticated cereals characteristically exhibit uniform, high rates of germination, while wild synaptosperms such as wild emmer have pronounced dormancy polymorphisms. A synaptosperm is a species that disperses more than one seed in each diaspore; wild emmer spikelets typically have two seeds. If both seeds germinate at once, their seedlings will compete. Selection, then, favors a somatic polymorphism in which one seed is non-dormant, and the other is dormant for perhaps a year (Zohary 1969; Blumler 1991, 1992a). Selection against non-dormancy should not be as severe as against indehiscence in the wild, so the trait should persist for a longer time period after the introgression has ceased. Other domesticated traits, discussed below, probably are selected against to a still slighter degree, and persist still longer, but on the other hand become less reliable indicators of introgression for precisely the reason that selection does not work strongly against them. By considering a range of such traits, one should be able to test whether introgression has occurred in a given population.

Finally, introgressed plants should exhibit a predictable spatial pattern. They should be more common in and around current or former cultivated fields, especially where cultivation abuts on untillable land that is good habitat for the wild species. Introgression is more likely to be significant also where the amount of cultivation is great in comparison with the size of the wild populations: theoretically, then, geneflow from the crop might overwhelm selection for wild traits. Wild populations can be sampled along transects running away from cultivated land, to determine if the putative introgressed alleles decrease with distance. If so, introgression is likely, especially if there is no corresponding environmental gradient along the transect.

Comparing wild emmer with durum and emmer

Jakubziner's (1932) monograph remains the most authoritative description of the morphological variation in emmer and durum, and is useful also because of its treatment of Palestinian durum landraces, which would be the most likely parents in introgression events. Durum and emmer are different from each other, especially in spikelet characteristics. In addition to the characters described in Jakubziner, I added a few cryptic (i.e. physiological rather than morphological) traits investigated by others. To compare with wild emmer, I examined the herbarium specimens at important repositories such as Edinburgh and the Hebrew University, and also visited a few populations in the field. While typical (*horanum*) wild emmer is not at all similar to durum, UJV varies in the direction of durum in several respects (Blumler 1994). Grain shape, glume shape, first glume tooth, glume pubescence, spikelet width and glutenin A1-1 allele all are at least occasionally like durum, while there are no characters for which UJV is demonstrably more similar to emmer. In general, UJV is highly variable but intermediate between durum and *horanum* wild emmer, as one would expect if it were the product of hybridization (Blumler 1994).

Box 1. Approaches to identifying introgression.

1. Morphological comparisons

      wild progenitor should be more similar to emmer than durum

2. Ecological considerations

      certain traits are likely to be adaptive in the wild, others in the cultivated field

3. Spatial pattern

      introgression is more likely in or around former cultivated fields

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The glutenin data of Levy and Feldman (1988) are particularly informative. Glutenin A1-1 is present in domesticated emmer, but absent in durum. It is almost always present in wild emmer, but is generally absent in UJV, which suggests that introgression from durum may have been massive. Of the 19 wild populations outside UJV that Levy and Feldman examined, glutenin A1-1 was 100% present in all but two: a population just south of UJV, and Majdal es-Shams. As mentioned above, Jakubziner (1932) reported *judaicum* from Majdal es-Shams. Both populations are in agricultural areas, whereas most wild emmer populations are on rocky slopes where cultivation could only have been practised in a few select spots. Interestingly, the glutenin A1-2 locus presents a different pattern: absent in most wild emmer populations, absent in durum and emmer, but present in bread wheat and in some UJV plants. Since Levy and Feldman did not study Palestinian

durum landraces, it would be interesting to determine if they also possess A1-2 alleles.

Ecological influences on introgression

As discussed above, a few domesticated traits such as indehiscence and lack of dormancy are selected against in the wild. On the basis of ecological research, I believe that several additional traits are selected against, though less strongly than indehiscence (Box 2). I believe, too, that a few domesticated traits are sometimes advantageous in wild environments (Blumler 1994). Most of these traits are spikelet characters, because of the importance of seed dispersal and self-implantation in the ecology of the wild plant. Zohary and Brick (1961) and Zohary (1969) described the 'arrow-shaped' spikelets of wild emmer, and pointed out that they are so structured as to enable them to drill into the soil where they are protected from predation until the fall rains initiate germination. The glumes tightly invest the two grains, which are elongate in order to fit into the arrowhead shape. I examined specimens that differ from typical forms in being more like domesticates. Any change to rounder grains, more grains per diaspore, or more divergent glumes makes the structure less streamlined and therefore, presumably, less able to drill into the soil.

I also investigated the drilling ability of the spikelets under various microenvironmental conditions (Blumler 1991). I found that the spikelets generally drill into soil cracks or adjacent to rocks or other obstructions where the vegetation has been mostly removed (e.g. under grazing); on the other hand, in more-or-less undisturbed conditions where the dead plants remain standing at season's end, the two awns of the spikelet tend to catch in the litter, and prevent the diaspore from penetrating all the way to the soil surface. Seedling establishment is nonetheless excellent under these circumstances, as the grains end up close enough to the surface that their roots can penetrate the soil after germination. Thus, it seems possible that the changes in spikelet morphology induced by introgression would be selected against where there is grazing, but might not be under undisturbed conditions. The somewhat more awkward spikelets of hybrids, with round grains or three grains, probably still can drop through litter to just above the soil surface, whereas they may be less efficient at drilling into cracks on bare ground. Further research is needed to test this hypothesis.

There are predictable effects of domestication on grain size and shape. As the spikelet is no longer needed to disperse the grains, the tightly investing glumes open up over the course of evolution, allowing the florets to expand outwards or to increase in number. Since grain size and shape reflect that of the floret (Millet 1986), the 'naked' grains such as durum are often round, whereas the glume wheats such as emmer remain elongate. Those species or varieties that increase the number of seeds per spikelet, such as bread wheat, produce relatively small grains, whereas those with fewer grains per spikelet produce large ones, such as some forms of durum. Thus, with introgression from durum, wild grain size is likely to increase.

But whether this will be selected against should depend on site conditions. In annual species, seed size is strongly correlated with site productivity, both among and within species (Blumler 1992b). While the within-species variation may be largely phenotypic, the variation between species is so great that it must be primarily genetic. On infertile sites, annuals have difficulty producing enough photosynthate to fill large seeds, whereas they should be able to produce small seeds relatively easily. Sinnott (1921) showed in cultivated annuals that seed size increases phenotypically as productivity (plant size) increases, eventually leveling off. I studied several Jerusalem wild emmer populations on hard limestone, where soil depth, and hence productivity, vary over short distances, providing a natural analogue to Sinnott's experiment (Blumler 1992b). Results were identical to his: grain size increased with plant height up to a point, and then appeared to level off (Fig. 1). However, some populations leveled off at a low mean grain weight (<20 mg), whereas others did not do so until they were considerably larger (>35 mg). The populations with low mean grain weight occurred on sites that were relatively low in productivity over most of the site, though with a few high-productivity pockets, whereas the larger-grained populations were on deeper, more productive soil with a few small areas of infertile substrate. When seeds from wild populations were planted in a uniform garden, however, there was no relationship, within populations, between weight of grain planted and grain produced. That is, the within-population variation was mostly phenotypic. The relevant implication is that the large grain size of most domesticated genotypes should be advantageous on fertile sites but not where productivity is low. Since most cultivated fields have deep soil, they are productive compared with natural stands of wild emmer. Thus, in the places where introgression is likely to occur, large grain size may not be disadvantageous, and may even be beneficial.

Box 2. Ecological aspects of introgression.

1. Dormancy

      selection for polymorphism within spikelet

2. Drilling ability of spikelet

      selection for elongate grains, parallel glumes, narrow spikelets, two seeds/spikelet, dehiscence

3. Productivity

      selective and phenotypic effects on grain size

4. Pigment

      selection for coleoptile pigment, glume pigment

Finally, it appears that there may be a selective advantage to anthocyanin and other pigments in wild plants, but not in domesticates. The ecology of anthocyanin is poorly understood and even less studied - one suggestion is that it makes plants less palatable to herbivores - but there is no question that loss of pigment is a feature not only of wheat domestication, but also of the domestication and evolution of many other crops. Exceptions occur when humans intentionally select pigmented forms for ornamental purposes (e.g. 'Sangre de Cristo' maize, amaranths). Most wild emmer populations are black glumed, with anthocyanin pigment present in various vegetative parts, often including the coleoptile. Most durum lacks pigment.

With these ecological considerations in mind, and also the morphological comparisons discussed in the previous section, we can construct a list of traits that are likely to be characteristic of domesticates but not of truly wild plants (Box 3). Included will be those characters controlled by genes linked to the traits of ecological concern. For instance, the rounding of the glumes that often occurs in durum because of the change from elongate to rounded grains typically is associated with specific changes in the glume teeth that seem likely to be of no selective value. Glume pubescence also is characteristic of durum, particularly the Palestinian landraces (Jakubziner 1932; Poiarkova and Blum 1983), and especially the varieties with rounded glumes, but it is difficult to understand how it could be adaptive. Wild emmer populations are mostly glabrous, but the sibling species *T. araraticum* is usually pubescent. It seems likely, therefore, that glume pubescence is a neutral or nearly neutral character. I noticed, during the course of my examination of herbarium specimens, that wild emmer with pubescent glumes occurs, without exception, in populations that show more reliable indicators of introgression such as rounded glumes or three-seeded spikelets. Consistent with this conclusion, Oppenheimer (1963) reported that pubescent glumed individuals of wild emmer are less dormant than those with glabrous glumes. Perhaps there may be pubescent individuals somewhere that are not the result of introgression but they have not been collected.

There are numerous additional traits, not listed in Box 3 because of insufficient data, that merit further investigation. For instance, glaucous glumes and absence of leaf sheath cilia both appear to be durum traits (Jakubziner 1932), but I have little information on their distribution in the wild. More speculatively, it seems possible that pale glumes, which are common in durum but infrequent though widespread in wild emmer, may be a reliable indicator of introgression. In my Jerusalem studies, for instance, I noticed that pale-glumed forms of wild emmer make larger grains and grow in more productive sites than populations that produce black glumes. I have yet to encounter a pale-glumed form of wild emmer that produces the 20-mg grains of some black-glumed types, except under stress.

Regardless, populations from UJV that I examined either in the field or the herbarium all exhibit more than one of the indicators listed near the top of Box 3. Possibly typical is the population at Migdal described by Jakubziner (1932), which included the varieties (with some peculiar variants) listed in Table 2. All of the peculiar variants are typical of durum. Of course, in this case there are no data on characters that he did not investigate, such as glutenin alleles.

Spatial analysis of UJV

As mentioned above, all UJV-type populations occur in close proximity to extensive areas of former durum cultivation. More precise spatial analysis of allele frequencies should allow a more rigorous test of the introgession hypothesis. Fortunately, this is possible because of the existence of a detailed data set from Ammiad, a kibbutz located at the former site of the Palestinian waystation of Jubb Yusuf. A multidisciplinary team has carried out detailed ecological and genetic studies of the population, located on karstic limestone hills that form the western boundary of UJV, as well as the adjacent UJV alluvium (Anikster and Noy-Meir 1991). The site is located only about 100 meters from the large hybrid swarm described by Zohary and Brick (1961) and D. Zohary (pers. comm.), but the Ammiad team (with the exception of Felsenburg et al. 1988) assumed that no plants in the population are introgressed. Plants were gathered along transects, and analyzed genetically, while ecologists characterized the four primary microenvironments occurring there. If UJV plants are truly a locally evolved race, adapted to the basalt and alluvium of UJV itself, and not to other environments, then UJV alleles should occur at Ammiad where transects extend into the alluvium, but only incidentally on the adjacent slopes, in microsites that mimic UJV. On the other hand, if UJV is the result of introgression, UJV alleles should decline with distance from the alluvium regardless of microenvironment. The full analysis will be reported in a separate paper. Here, I will discuss only the most dramatic evidence.

This evidence comes from Transect 'C', which is in extreme karstic terrain. Noy-Meir et al. (1991) concluded that the microenvironment along Transect C differs greatly from the microenvironment on the UJV alluvium. In fact, according to Noy-Meir et al. these are the two most differentiated environments at the site. However, the base of Transect C is geographically close to the alluvium of a wadi that runs into UJV, and cultivation would have been practised in the wadi in the past (D. Zohary, pers. comm.). Thus, on ecological grounds one would predict C to have few if any UJV-type plants, while it might have many such plants if the introgression hypothesis is correct.

In fact, and in contrast to the remainder of the population, the section of C nearest to the alluvium (accessions 160-180) is laden with plants that have many UJV alleles (Table 3). As one goes up the transect away from the wadi, the UJV alleles suddenly drop out at accession 160, which is half way up a limestone cliff. The accessions on the transect above the cliff are almost completely devoid of UJV alleles, suggesting that the cliff forms a topographic barrier to their dispersal upslope from the wadi. Gene frequencies in lower C are very similar to the two UJV populations that have been intensively studied, Yehudiyya and Tabgha (Table 3). Lower C plants also resemble UJV morphologically. In contrast, the remainder of the Ammiad population exhibits gene frequencies that are very similar to non-UJV populations. Given that C is ecologically so dramatically different from UJV, it is difficult to explain this pattern as the result of natural selection. Moreover, if selection favors UJV alleles on this particular karstic site, then UJV plants should turn up on extreme karstic limestone elsewhere as

well. Karstic limestone is extremely widespread in Palestine, and commonly supports wild emmer populations, but as far as is known, does not support UJV plants elsewhere.

Fig. 1. Relationship between plant height and grain weight in a population of wild emmer in Jerusalem (Blumler 1992b). Seed weight appears to increase linearly up to a plant height of approximately 75 cm and a weight of 21 mg; it appears to be stable at greater plant heights.
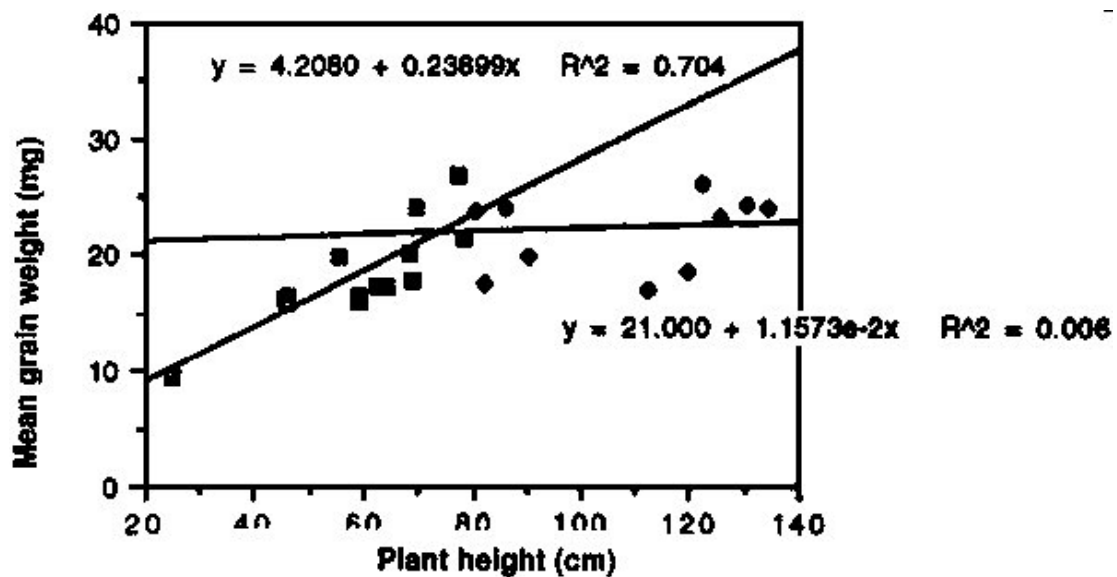
Box 3. Some morphological and other indicators of introgression in wild emmer.

Traits are ranked according to the reliability with which they suggest that introgression has occurred. Indehiscent plants are almost certainly introgressed, whereas plants that produce large grains may not be.

Indehiscence	Poorly developed second glume tooth
Rounded grains	Absence of glutenin A1-1
Three-grained spikelets	Absence of pigment
Low grain dormancy	Short grain brush
Pubescent glumes	Large grains
Curved glume tooth	

Table 2. Some varieties of wild emmer in a collection from Migdal in UJV (Jakubziner 1932).

Variety	Glumes	Peculiar variants
horanum		
kotchii	white, glabrous	glaucous glume
palestinicum	white, pubescent	
judaicum		
arabicum	white, glabrous	glaucous glume with long curved tooth; glabrous leaf sheath
vavilovi	black, glabrous	long curved apical tooth
fulvovillosum	white, pubescent	large tooth

Although the C plants are very similar to those from UJV populations, they are not identical; for instance, compare allele frequencies at loci Pgi-A, Pgi-B and Glu-A1-1 in Table 3. Nor are Yehudiyya and Tabgha identical to each other. At most loci there is a characteristic allele that predominates throughout Palestine, and also at Ammiad, but not in UJV. Within UJV, on the other hand, the predominant allele at any given locus is highly variable from site to site, and alleles sometimes are common at one site but absent at others. This is as one would expect if UJV resulted from repeated introgression events with diverse durum landraces, but makes little sense if UJV is the result of natural selection in a purely wild setting. UJV appears ecologically fairly uniform, in contrast to karstic limestone sites where soil depth, moisture and shading typically vary greatly over short distances.

Discussion

While these results are still preliminary, the convergence of several lines of evidence strongly indicates that massive introgression has occurred in UJV, giving rise to the UJV 'race' of wild emmer. Does this mean that UJV is not the locus of domestication? At present, we have no information that bears on that question. The evidence for massive introgression at

UJV merely means that its populations are no more or less likely than other wild emmer populations to be the progenitor. UJV-type plants reported elsewhere, such as on Mt. Hermon, also seem to be introgressed. If pale glumes occur in the wild only after introgression, then many additional populations and subpopulations have been altered by interactions with domesticated wheat. Introgression appears to have been more massive in Palestine than elsewhere in wild emmer's range. This may reflect the abundance of low-elevation, warm-winter, highly productive habitats in Palestine, though it may also be an artifact of the greater density of exploration and scientific study in Palestine compared with other parts of the Fertile Crescent.

Stands of wild cereals in and around UJV are known to be especially productive (Harlan and Zohary 1966), so large grain size might be present naturally in wild populations, or alternatively, might be selected in the wild after introgression from domesticates. On the other hand, most wild emmer populations occur on much less productive sites, where introgression of genes for large seed size might be selected against. This is a possible explanation for the apparently massive introgression in UJV, and the smaller degree of introgression elsewhere. Moreover, the elimination of Palestinians from UJV in 1948 was followed by a long period of limited exploitation of the land. Settlers initially grazed the region very lightly because they were unsure how much pressure the vegetation could support. Characters such as large seed size and low dormancy should be favored under relatively undisturbed conditions when stands are dense. Recently, grazing pressure has been increasing, and wild emmer populations appear to be declining in consequence. Under these circumstances, selection against domesticated traits may be more severe.

That introgression apparently has been so massive in wild emmer, a non-weedy species, raises questions concerning the extent of introgression in other wild crop relatives. Considerable concern and debate exists about the likelihood that genetically engineered crops might pass the engineered genes to wild relatives, with subsequent effects on ecosystems. Ecologists tend to express serious concern (Tiedje *et al.* 1989), whereas geneticists sometimes dismiss the possibility, perhaps because of an underlying assumption that wild plants are already well-adapted to natural environments and therefore unlikely to be improved in fitness by geneflow from domesticates. But the example of wild emmer suggests that genes from cultivated plants can indeed affect the genetic make-up and perhaps the fitness of wild plants.

Geneticists have studied wild emmer to address theoretical issues, such as the comparative roles of natural selection and neutral mutation in evolution. Nevo *et al.* (1982, 1986) concluded that natural selection was at least partly responsible for allozyme distribution patterns, but Nevo's statistical methodology is known to be invalid (Heywood and Levin 1985). In a more rigorous series of experiments, Golenberg (1986, 1989) found no evidence for an adaptive basis for allozyme distribution in UJV. Neither Nevo nor Golenberg considered the possibility that durum genes might have introgressed into their populations. The evidence presented here for massive introgression suggests that the odd electrophoretic variants in UJV are contaminants from durum, currently hitchhiking on other traits upon which selection is working. Similarly, the Ammiad study site was selected in part because of its high genetic variability; but when the putative introgressed alleles are subtracted, genetic diversity becomes very low (Blumler, unpublished). Consequently, the assumption of the researchers that there has been local-scale adaptation to differing microenvironments at Ammiad (Nevo *et al.* 1986) is probably incorrect.

Conclusion

To return to the agricultural origin question, one implication of these results is that introgression may be more massive than realized in other wild progenitors, such as einkorn and bean, as well. Einkorn probably has not been cultivated near Karacadag for some time, and would have been rare for a still longer period, so any introgression that might have occurred presumably would have been much more ancient than the introgression in UJV. Assume for the sake of argument that massive introgression did occur, say, 3000 years ago. By now, the most obvious indicators of introgression, such as indehiscence, would have been selected out of the wild populations. Only more-or-less neutral introgressed alleles might still be present. But since the analysis of Heun *et al.* (1997) was of DNA that probably is more-or-less neutral, it does not seem possible to reject introgression entirely. I should emphasize that I am quite comfortable with the conclusions of Heun *et al.* (*1997)*, and also with those of Gepts (this volume), because they conform to my own views on agricultural origins; for instance, Gepts' report of a northwest Argentinian origin for Andean common bean was anticipated by my paper (Blumler 1992a). But at the same time, given the amount of introgression I am finding in wild emmer, I cannot but feel that the introgression issue needs to be addressed more fully in all other crops as well.

Table 3. Allele frequencies in *Triticum dicoccoides* in Palestine[†].

Locus	Ammiad		Transect C 160-180		Yehudiyya (UJV)		Tabigha (UJV)[‡]		Other Palestine		Ammiad, exc. 160-180	
	N	Freq.	N	Freq.	N	Freq.	N	Freq.	N	Freq.	N	Freq.
6Pgd-2	191		21		96		39		354		170	
M		0.890		0.524		-		0.333		0.958		0.935
S		0.110		0.476		1.000		0.667		0.006		0.065
Pept-3	146		8		96		0		49		138	
M		0.918		0.500		0.016		-		1.000		0.942
S		0.082		0.500		0.984		-		-		0.058
Pgi-A	230		20		39		37		375		210	

F	0.387	0.550	0.026	0.189	0.115	0.371
M	0.583	0.250	0.974	0.811	0.797	0.615
G	0.030	0.200	-	0.088	0.014	
Pgi-B	230	20	39	40	378	210
M	0.252	0.650	-	-	-	0.214
S	0.748	0.350	1.000	1.000	1.000	0.786
b-Gluc-A	217	17	39	40	361	200
M	0.843	0.294	-		0.914	0.890
N	0.157	0.706	1.000	1.000	0.053	0.110
b-Gluc-B	216	17	96	0	49	199
F	0.194	0.765	1.000	-	0.020	0.145
M	0.806	0.235	-	-	0.980	0.855
Mdh-1A	224	19	96	40	369	205
F	0.085	0.316	1.000	0.950	0.014	0.064
M	0.915	0.684	-	0.050	0.986	0.936
Glu-A1-1	178	21	33	88	345	157
a	0.101	0.857	0.727	0.568	0.046	-
e	0.022	-	0.273	0.284	0.046	0.025
k	0.573	-	-	-	0.099	0.650
l	0.303	0.143	-	0.011	0.220	0.325
Glu-B1-1	178	21	33	88	345	157
g	0.129	0.857	0.000	0.148	0.058	0.032
Glu-B1 -2	178	21	33	88	345	157
l	0.129	0.857	0.000	0.125	0.043	0.032
Pept-1B	208	11	96	40	374	197
F	0.038	-	0.995	0.675	0.048	0.040
M	0.962	1.000	0.005	0.325	0.952	0.960
Aat-2a	231	21	39	40	378	210
F	0.009	-	0.385	0.050	0.021	0.010
M	0.991	1.000	0.615	0.950	0.979	0.990
Acph-3	231	21	39	40	378	210
F	0.022	0.048	0.590	0.975	0.003	0.019
M	0.957	0.952	0.410	0.025	0.947	0.957
S	0.022	-	-	-	0.050	0.024

[†] From Nevo *et al.* (1982, 1986); Golenberg (1986); Levy and Feldman (1988).

[‡] Allele frequencies of HMW glutenin loci calculated as mean of S. Almagor, NW Almagor and S Ammiad (Levy and Feldman 1988).

There is a great deal of emphasis today on molecular approaches to phylogeny, and rightfully so, but at times this has had the unfortunate effect of causing a neglect of traditional morphological analysis. Attention to morphology was an essential component of the research discussed here, and must continue to be if we are to obtain a clearer picture of introgression in wild emmer. Also essential will be further ecological research, for instance, into the adaptive value of anthocyanin or the drilling abilities of spikelets of different morphologies. My own investigation into the latter (Blumler 1991) was merely synoptic. In fact, it is fair to state that ecological research is the weak link in agricultural origins studies. In comparison, both archaeological and genetic investigations are going great guns, despite funding problems, difficulties of access to crucial locations, and so on. Until we understand the ecology of wild progenitors better, it will be difficult to be certain where they grew, in what abundance, and how hunter-gatherers impacted them.

Acknowledgments

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The Variation of Grain Characters in Diploid and Tetraploid Hulled Wheats and its Relevance for the Archaeological Record - K. Hammer and C.-E. Specht

Introduction

Today, hulled wheats can be considered as underutilized or neglected crops (Padulosi *et al.* 1996). In past societies hulled wheats had a great importance as staple crops. The declining importance in connection with the preferred use of naked wheats and other influences led to a decline in hulled wheats which have been only relic crops or were considered extinct at the beginning of the 1980s. New accessions from the Mediterranean area proved that hulled wheats are still cultivated in remote places. The conservation of *Triticum monococcum* L. and *T. dicoccon* Schrank in field reserves of south Italy was proposed in 1984 (Perrino and Hammer 1984) and new interest for these traditional crops developed, leading to a certain increase in the growing area. Material was collected and preserved *ex situ* in genebanks. Large living collections were established, characterized and evaluated, which led to a better knowledge of the variation in hulled wheats.

Material and methods

The material for this study came from the Gatersleben genebank. Diploid (*T. monococcum, T. boeoticum* Boiss. and *T.*

urartu Thum. ex Gandil.) and tetraploid (*T. dicoccon, T. dicoccoides* Körn. ex. Schweinf.) hulled wheats were selected for this study.

The material investigated is shown in Table 1. For all accessions the thousand-grain weight (TGW) was determined by weighing 100 grains three times and calculating the value for 1000 seeds. The husks were manually removed. Grain length and thickness were determined for selected accessions representing the extremes in TGW. The statistical calculations were done with a computer using the program PLABSTAT (Utz 1991).

Table 1. Material used for the studies.

Species	Number of accessions	Number of botanical varieties according to Dorofeev *et al.* (1979)
Triticum monococcum	125	11
Triticum boeoticum	29	16
Triticum urartu	8	4
Triticum dicoccon	139	28
Triticum dicoccoides	24	14

Results and discussion

There is a great variation in the material investigated. *Triticum monococcum* has a higher grain weight than its wild progenitor *T. boeoticum* because of domestication. The wild *T. urartu,* which also plays an important role in the evolution of the cultivated wheats, is comparable to *T. boeoticum.* On the tetraploid level we find similar relations with the cultivated *T. dicoccon* and its wild progenitor *T. dicoccoides* but the overlap is much higher (Table 2).

There is a tendency for the grains to be heavier in tetraploid wheats than in diploid ones. But, again, there is an overlap between the higher weight classes of *T. monoccocum* and the lower classes of *T. dicoccon* (Table 2, see also Fig. 1). Therefore, weight of grain, even when determined on a relatively large number of seeds, which is usually not available in archaeological excavations, may be useful only for lower seed weight classes in *T. monococcum* (about 0.025 g/seed) and higher seed weight classes in *T. dicoccum* (about 0.04 g/seed). The loss of weight during carbonization of this material could be easily determined experimentally.

On the basis of weight data, extremes have been selected for the determination of grain length and grain thickness which are easier to investigate in archaeological material. The reduction by carbonization can be seen by comparison of our data with those of Kroll (1992), e.g. carbonized einkorn grain length of 3.3-5.7 mm minimum and in our data, 6.1-9.0 mm (Table 3).

Of all species studied, *T. dicoccoides* had the longest seeds (Table 3). A general increase in length during domestication did not occur. On average, *T. dicoccum* is shorter-seeded than *T. monococcum.* Grain thickness is a better character for showing evolutionary tendencies, and accordingly *T. dicoccum* has thicker seeds than *T. monococcum.*

More difficult is the distinction between emmer and emmer-like einkorn. One of the first authors to compare the variations of recent and fossilized materials was E. Schiemann (1940). She came to the conclusion that there is a certain amount of two-grained spikes in recently collected einkorn material. In this case one or both of the grains can keep their typical einkorn shape. In 1996 a botanical variety of einkorn was described which is typically two-grained with well-developed einkorn kernels (var. *clusii* Szabó et Hammer from Transylvania, Szabó and Hammer 1996). Also the archaeological literature increasingly reports two-grained einkorns (van Zeist and Bakker-Heeres 1982; Kroll 1992). Interestingly these findings extend from the Balkans to the Levant with outposts (?) to more central European areas (Kreutz, pers. comm.). If we could assume that the wild two-grained einkorn (*T. boeoticum* subsp. *thaoudar* (Reut. et Hausskn. Grossh.) should be the progenitor of the two-grained cultivated einkorn, its more eastern distribution in comparison with the typical one-grained wild einkorn subsp. *boeoticum* (see Dorofeev *et al.* 1979) would be difficult to explain. More reliable is a positive selection within the seed trait which also intergrades in the wild progenitor (Harlan and Zohary 1966; Zohary 1969). Similar problems occur with one-grained spikelets of *T. dicoccoides* in comparison with typically one-grained *T. boeoticum* (Pasternak, pers. comm.).

Our data show tendencies but they cannot provide a definite distinction, especially in cases of two-grained einkorn as compared with emmer. Many recent einkorn spikes have been examined and show a marked tendency to two-grained forms. This tendency is especially high in the newly described *T. monococcum* var. *clusii.* Some indications for the distinction of einkorn and emmer can be obtained from the kernel thickness but also from more detailed studies of grain characters. According to Nesbitt and Samuel (1996), einkorn grains have a typical spindle shape with pointed apex and pronounced ventral convex curve as opposed to emmer grains with a blunter apex and straighter sides. Moreover, Kroll (1992) reports on a small depression in the ventral outline. Our data confirm the statement of Kroll (1992) that it is not possible to distinguish emmer-like einkorn grains from emmer grains by metrical means only and also it is impossible to separate them accurately by morphological features.

Table 2. Thousand-grain weight (TGW in g) for diploid and tetraploid hulled wheats.

	x ± s	Min. - Max.	Number of accessions

Triticum monococcum	28.822 ± 3.401	19.90 - 38.40	125
Triticum boeoticum	15.931 ± 2.629	11.60 - 19.80	29
Triticum urartu	16.362 ± 2.462	10.90 - 18.90	8
Triticum dicoccum	41.260 ± 7.713	29.80 - 67.80	139
Triticum dicoccoides	31.450 ± 7.379	20.20 - 51.20	24

Table 3. Grain length (mm) and grain thickness (mm) for diploid and tetraploid hulled wheats.

	Length (x ± s)	Min. - Max.	Thickness (x ± s)	Min. - Max.	No. of grains
Triticum monococcum	7.88 ± 0.72	6.1 - 9.0	2.25 ± 0.35	1.5 - 3.0	60
Triticum boeoticum	7.80 ± 0.82	6.9 - 10.0	1.68 ± 0.22	1.4 - 2.2	40
Triticum urartu	8.39 ± 0.68	7.0 - 10.0	1.53 ± 0.33	0.9 - 2.1	50
Triticum dicoccon	7.59 ± 0.86	6.0 - 9.0	2.95 ± 0.39	2.0 - 4.1	60
Triticum dicoccoides	9.24 ± 0.86	7.0 - 11.0	2.30 ± 0.48	1.5 - 3.8	40

Fig. 1. Variation and frequency of thousand grain weight (TGW) in *Triticum monococcum* and *Triticum dicoccon*. In the class 28.1-30 g, two accessions of *Triticum monococcum* are not visible.

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Utilization of Ancient Tetraploid Wheat Species for Drought Tolerance in Durum Wheat (Triticum durum Desf.) - A. Al Hakimi and P. Monneveux

Introduction

The variability of drought tolerance related traits is rather limited in durum wheat and hence interspecific crosses would seem to be a good tool to introduce such traits into durum wheat. Interspecific crosses between durum wheat and the other

tetraploid species of the *Triticum* genus represent a promising and more rapid path toward this objective. Arguments for extensive use of wild and cultivated tetraploid wheats in durum wheat breeding have been previously discussed (Grignac 1965; Joppa and Williams 1988; Damania *et al.* 1988; Al Hakimi *et al.* 1994).

The use of ancient and obsolete tetraploid *Triticum* species to incorporate some characteristics lacking in the modern commercial durum varieties has been suggested by several breeders (Damania *et al.* 1992). However, Clarke and Townley-Smith (1984) pointed out the need for backcrosses to recover the yield potential of the recurrent parent. Moreover, double or three-way crosses may also be useful for transferring desired traits to adopted genotypes.

Genetic variation for drought-resistance attributes has been observed in obsolete tetraploid wheat forms (*T. dicoccum, T. carthlicum, T. timopheevi* and *T. polonicum*). These include maintenance of leaf water potential (LWP), proline content (Pro), soluble sugar content (SSC), photochemical quenching of chlorophyll fluorescence (qQ), relative water content (RWC), chlorophyll content (chl), root growth and plant development or morphological attributes such as flag leaf area, leaf orientation, tiller number, yield and yield components (Damania *et al.* 1992; Al Hakimi and Monneveux 1993). Genetics of morphophysiological traits involved in resistance are less well known and complex interactions between these traits have to be further investigated (Blum 1993).

Yield improvement in durum wheat as in many other crops has been achieved through direct selection for absolute performance. However, critics of this approach have always pointed out that an understanding of the mechanisms (morphological and physiological) that might be correlated with or contribute to drought resistance is essential to the success of breeding varieties for areas where water is limited. These critics have also suggested that more gains in yield can be achieved rapidly and predictably if these morphophysiological mechanisms that contribute to drought resistance are better understood. Mechanisms that enable plants to adapt to moisture stress are multiple and a few of these are considered in this study.

Root architecture in response to water stress has been clearly established in cereals, especially in durum wheat (Benlaribi *et al.* 1990); the required root architecture can, however, vary in relation with the type of drought stress (Ali Dib and Monneveux 1992). Although selection and breeding for desirable root characteristics associated with drought resistance have been practised in wheat (Hurd 1974) and other cereal species (Taylor and Yamauchi 1991), the genetics of root characters have not been fully investigated. A high variability has been observed in the *Triticum* genus for several root characters, including the quantity of roots (Mac Key 1979; Robertson *et al.* 1985), but this variability has not been exploited systematically in wheat improvement.

Relative water content (RWC) is a physiological trait frequently proposed as a criterion in selection for drought resistance (Acevedo 1987; Schonfeld *et al.* 1988). RWC is influenced by osmotic adjustment (Morgan and Condon 1986) and by water absorption and transpiration (Schonfeld *et al.* 1988).

Theoretical considerations (Farquhar *et al.* 1982) as well as experimental data (Farquhar and Richards 1984; Hubick and Farquhar 1989; Acevedo 1993) have shown that variations in water-use efficiency should be associated with differences in the ability of plants to discriminate against ^{13}C compared with ^{12}C during CO_2 diffusion and fixation. Genetic variations in carbon isotope discrimination (Δ) have been observed in bread and durum wheat (Farquhar and Richards 1984; Condon *et al.* 1990; Ehdaie *et al.* 1991; Gate *et al.* 1992; Araus *et al.* 1993), but information is scarce concerning related species.

The objectives of the present study were to: (1) evaluate the genetic variability and describe the behavior of some morphophysiological traits related to drought resistance in ancient and obsolete tetraploid wheat species, (2) introduce these traits into improved varieties by interspecific crosses, (3) determine the potential of indirect trait selection for improving drought resistance, grain and biological yield under stress, using divergent selection in F_2 and F_3, (4) determine the genetic control of these traits, broad and narrow sense heritability response to selection and realized heritability, and (5) investigate the possibility of using ancient and obsolete tetraploid species to improve abiotic stress as well as grain quality.

Material and methods

Some accessions of tetraploid species (Table 1), identified for their special characteristics in improvement of drought resistance, were used in a physiology-based crossing program. Crosses obtained were evaluated in F_2 population by two methods: (1) indirect selection for various drought resistance related traits (divergent selection), and (2) direct selection for yield by using the 'F_2 progeny' method proposed by Smith (1987).

Divergent selection was applied by selecting groups of plants with high and low value of the trait in F_2 and F_3. Traits measured were: (1) RWC evaluated as the method describe by Barrs (1968), under greenhouse conditions; three crosses were involved in this study; (2) chlorophyll fluorescence (qQ) after Havaux and Lannoye (1985), under greenhouse conditions in two crosses; (3) root attributes were assessed in hydroponic conditions after the method discussed by Al Hakimi (1995), under the greenhouse in one cross, and (4) kernel carbon isotope discrimination (A) as described by Hubick *et al.* (1986) for evaluating water-use efficiency (WUE). The ratio of carbon isotope (R = $^{13}C/^{12}C$) was analyzed by using a multiple-collector mass spectrometer connected to an element-analyzer, which allowed the 'on-line' analysis of 50 samples per day.

Agronomic and morphological characters, such as grain yield (GY), biomass production (BP), plant height (PLH), harvest index (HI), growth vigor (GV), days to heading (DH), spike length (SL), spike shape (SSH), number of spikelets/spike

(NSP/S) and number of grains per spike (NG/S), were also assessed. Heritability was calculated in the broad-sense (h^2b) according to the formula:

$$hb = [\sigma^2 F_2 - (\sigma^2 P_1 + \sigma^2 P_2)/2)]/\sigma^2 F_2$$

and in the narrow sense (h^2n) as parent-offspring regression (Smith and Kinman 1965). Heritability (h^2r) was calculated according to Falconer (1989) as the ratio of selection in F_3 to selection differential in F_2, between the two divergent groups mentioned above.

$$h^2r = (HF_3 - LF_3)/(HF_2 - LF_2)$$

where H and L refer to the mean values of the (trait +) and (trait -) in F_2 and F_3.

Table 1. Crosses used in direct selection for yield and indirect selection for physiological traits.

Crosses	Abbreviation	Traits
T. dicoccum norcicum x *T. durum* 'Cham 1'	Tdi1 x Ch1	RWC&qQ[†]
T. dicoccum fuchsii x *T. durum* 'Om Rabi 5'	Tdi2 x OR5	Root
T. dicoccum semicanum x *T. durum* 'Om Rabi 5'	Tdi3 x OR5	†
T. polonicum pseudochrysospermum x 'Cham 1'	Tp9 x CM	RWC&qQ[†]
T. polonicum pseudochrysospermum x 'Om Rabi 5'	Tp9 x OR5	D[†]
T. polonicum Hadrache x *T. durum* 'Cham 1'	Tp11 x Ch1	†
T. carthlicum stramineum x *T. durum* 'Cham 1'	Tc12 x Ch1	RWC[†]
T. durum leucomelan x *T. polonicum* 'Hadrache'	Td21 x Tp11	†
T. durum leucomelan x *T. carthlicum fuligi*	Td21 x Tc14	†

[†] Direct selection for yield.

Results and discussion

Genetic variation for some morphophysiological traits related to drought resistance in ancient and obsolete tetraploid wheat species has been observed:

- *T. dicoccum* shows some interesting characteristics, including grain yield, biomass production, root growth, plant height, reduction of flag leaf area under water stress, high relative water content (RWC) and leaf water potential (LWP) which were recorded in some accessions under field and greenhouse conditions.

- *T. polonicum* has a high peduncle, high spike fertility, high 1000-kernel weight, good superficial rooting pattern; low variation for RWC, leaf area, chlorophyll content (chl), chlorophyll fluorescence (qQ), and high sugar accumulation which were registered under water stress; in addition *T. polonicum* is characterized by good grain quality.

- *T. carthlicum* is characterized by good tillering ability, good spike fertility, low leaf area; under water stress, high variation was observed for LWP but RWC, chl and qQ maintained low variation, and high level of SDS and protein content.

- *T. timopheevi* show erect and thin leaves, good root growth, high number of grains per spike, and high protein content.

- Durum wheat (*T. durum*) and bread wheat (*T. aestivum*) were characterized by high grain yield and harvest index; they maintain a high LWP, but RWC, chl and qQ are strongly affected by drought.

Genetic studies show that physiological traits (RWC, qQ, A) and root characteristics are under complex genetic control; broad sense heritability was found to be high but narrow sense heritability and response to selection were low in the case of root parameters and qQ (Table 2). Heritability figures obtained (which represent a good indicator of the selection efficiency) showed that RWC, A and root number could be used as selection criteria in plant breeding programs to improve water-use efficiency and to facilitate the development of cultivars adapted to arid environments.

Tetraploid wheats used in this study differed for kernel Δ (Δ value was 12% lower in the *T. polonicum* than in the *T. durum* accession). These results reflect the importance of using the ancient and obsolete tetraploid wheat with low Δ (high water-use efficiency) for improving drought resistance in high-yielding durum wheat varieties. Heritability was high for this trait (Δ) and involved dominance effects. However, narrow-sense heritability was found to be of intermediate value, which suggests that additive effects are involved in the expression of this trait. These results are in agreement with those of Ehdaie and

Waines (1994).

Correlations between Δ and biomass or grain production vary as a function of climate. Low Δ (greater water-use efficiency) was associated with higher grain production (r = -0.26**) and increased biomass accumulation under water stress (season with low precipitation, 373 mm) which was contrary to the results (positive correlation, r = 0.34***) obtained during the season with high precipitation (632 mm) in F_3. These results clearly indicate that climatic conditions and earliness due to high rainfall strongly affect the relationship between Δ and grain yield.

Evaluation of lines selected in F_4 and F_5 under field conditions in different locations for different morphological traits, yield and yield components shows that populations derived from interspecific crosses and selected for high RWC and low Δ had greater drought resistance, since they demonstrated early growth vigor, high harvest index, high grain yield and biomass production compared with those populations selected for low RWC and high Δ (results not presented here).

Direct selection for yield confirmed that early generation selection in F_2 and F_3 populations produced some lines which performed better than their parents under both water-stressed and optimal conditions. The evaluation for grain quality of F_3 lines shows that high SDS sedimentation value, high protein content and high 1000-kernel weight were incorporated from ancient and obsolete tetraploids into durum wheat lines (Table 3). Results presented in Table 3 indicate that high protein content and SDS sedimentation values were obtained in the crosses between a durum wheat landrace from Iraq and a *T. carthlicum* accession, and in the crosses between *T. dicoccum* and the durum wheat variety 'Om Rabi 5'. Protein content was higher in all the tested interspecific progenies than in the durum wheat check ('Om Rabi 5'), and furthermore, some lines reached higher grain yield and 1000-kernel weight than this check.

Table 2. Broad and narrow sense heritability and realized heritability for different morphophysiological traits in durum x ancient/obsolete tetraploid wheat crosses.

Attribute	h^2b	h^2n	h^2r
Relative water content (RWC)	0.73	0.59	0.91
Photochemical quenching (qQ)	0.54	0.12	0.28
Carbon isotope discrimination (D)	0.48	0.37	0.57
Root number	0.63	0.10	0.10
Root number more than 30 cm	0.91	0.49	0.43
Depth (cm)	0.66	0.12	0.23
Root volume (cm^3)	0.75	0.10	0.11

Table 3. Number of F_3 lines derived from interspecific crosses, evaluated for grain yield (G) and grain quality parameters (protein content, SDS sedimentation test, and 1000-kernel weight (TKW))

Varieties/crosses	No. of F_3 lines	Protein content (%)	Sediment test (SDS)	Grain yield (g)	TKW (g/m^2)
T. durum (Cham 1)	6	11.8 ± 0.3	21.0 ± 2.0	548 ± 82	41 ± 0.3
T. dicoccum 1	2	12.0 ± 0.4	19.0 ± 0.3	704 ± 102	41 ± 0.7
(Tdi1xCh1) F_3	22	11.1 ± 0.7	19.2 ± 2.3	662 ± 150	46 ± 4.0
T. polonicum 9	2	13.1 ± 0.3	24.0 ± 0.1	481 ± 108	52 ± 0.9
(Tp9xCh1) F_3	20	11.8 ± 0.8	24.1 ± 4.1	525 ± 151	47 ± 4.5
T. carthlicum 12	2	12.4 ± 1.0	40.0 ± 5.0	547 ± 91	31 ± 0.3
(Tc12xCh1) F_3	11	12.8 ± 2.4	28.4 ± 6.3	328 ± 218	36 ± 3.9
T. polonicum 11	4	10.5 ± 0.5	24.3 ± 1.2	330 ± 102	42 ± 0.6
(Tp11xCh1) F_3	13	9.6 ± 0.8	20.4 ± 3.0	422 ± 93	41 ± 4.3
(Td 21xTp11) F_3	28	11.3 ± 1.4	32.0 ± 6.5	428 ± 112	41 ± 3.5
T. durum (Td21)	3	11.2 ± 1.2	36.0 ± 3.0	458 ± 69	48 ± 2.1
(Td21xTC14) F_3	14	11.9 ± 1.2	31.6 ± 4.7	400 ± 88	37 ± 3.4
T. carthlicum 14	2	13.0 ± 1.1	29.0 ± 3.0	312 ± 98	30 ± 1.0
T. durum ('Om Rabi 5')	2	12.4 ± 0.3	25.5 ± 0.5	596 ± 126	44 ± 3.8
(Tdi3xOR5) F_3	22	12.4 ± 1.1	24.6 ± 4.4	547 ± 87	43 ± 3.1
T. dicoccum 3	2	12.3 ± 0.2	25.0 ± 5.0	468 ± 44	34 ± 2.1

Conclusions

Evaluation of ancient and obsolete tetraploid wheats for drought resistance related traits indicates that many accessions

are potentially useful for the improvement of drought resistance in durum wheat varieties. The ability to maintain the relative water content (RWC) under water stress, a criterion closely related with osmotic adjustment, and carbon isotope discrimination (Δ) appear to be of a polygenic nature and highly heritable. Moreover, positive transgressive effects have been observed in some interspecific crosses. All these results, as well as the possibility to introduce grain quality characteristics such as protein content into durum wheat through interspecific crosses, encourage the use of ancient and obsolete tetraploid wheats in durum wheat improvement.

Heritability and selection response of morphophysiological traits related to drought resistance were evaluated and the impact of the divergent selections on morphological and agronomical characters was studied under field conditions. Results indicate that selecting for the morphophysiological traits related to moisture stress, such as relative water content and carbon isotope discrimination, is possible, since they showed high heritability values. However, the effect of selection for these traits on yield stability has to be further investigated. Improvement of yield is possible, by both direct and indirect selection.

Populations selected from these studies were evaluated in preliminary yield trials in Yemen. Preliminary results indicated that the use of related species combined with a bulk modified breeding method is promising not only for increasing yields in durum wheat in drought-prone environments but also to improve durum wheat yield stability across a wide range of climatic conditions. However, further studies are needed in this regard to study the long-term behavior of progenies of these crosses.

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Archaeobotanical Evidence for Evolution of Cultivated Wheat and Barley in Armenia - P.A. Gandilian

Introduction

Geographically the territory of the Republic of Armenia is part of a larger region conventionally called the Armenian Upland (Abich 1882). In the past Armenia was the place of origin of the ancient Armenian nation (Urartu) that encompassed the whole upland. The Armenian Upland acts as a kind of wedge between the Iranian and the minor-Asiatic mountainous structure which is above these highlands by almost 500 m. That is why the Upland is sometimes also called the Mountain Island. Its area is more than 300,000 km^2 and the mean altitude is 1700 m asl. The territory of the Republic of Armenia is 29 740 km^2 (nearly 10% of the former historic Armenia realm). However, almost all of the Upland's natural environments,

relief and climatic features as well as plant and animal diversity are replicated within the country.

The Armenian Upland is an integral part of the West Asia region which is widely known as one of the primary centers of human culture. Humans have been living here since the early Stone (lower Palaeolithic) Age. This land attracted people not only for its favorable environment (such as climate, suitability for building settlements, etc.), but also for its character and specific features of vegetation. It is known that primitive communities established themselves predominantly in areas rich in biodiversity of vegetation, including a wide range of edible plants. A large part of the Armenian Upland includes the Armeno-Iranian province which is characterized by rich and unique flora with high generic and specific endemism (Takhtajan 1978).

In the scriptures and ancient books Armenia with its regions is called a "fertile country" and "warehouse of the wheat and barley", among other names. There is a mention in manuscripts of wheat and barley being taken from Armenia by Assyrian kings after their conquests during the 9th to 8th centuries BC. For instance, Assyrian King Sargon II (722-705 BC) conquered many countries and forced their people to pay taxes with domesticated animals. However, when Sargon II overran Urartu (ancient Armenia) he noticed large warehouses full of wheat and barley. "I opened the doors of these warehouses and fed my soldiers with a lot of grains," said he (Thureau-Dangin 1912).

The archaeobotanical materials from Armenia are of great importance for the study of the origins of crops and domestication of plants in the Near East. There is strong evidence to suggest that wheat (*Triticum* L.) and barley (*Hordeum* L.) have been cultivated in Armenia from the earliest times. Charred remains of spikelets and grains of wheat and barley have been found in Armenia side by side with other archaeological finds related to human culture of that time.

Many scientists accept that the place of wild plant domestication and the transformation to cultivated forms must lie within the area of the plant's natural habitat. Helbaek (1959) wrote that the ancient crops of the Old World were wheat and barley. Wild progenitors of wheat, barley and rye are found in Armenia even today. According to the archaeologist Sardaryan (1967) wheat was found in Neolithic strata of settlements (6th millennium BC) and barley grains were found in clay pots, and also in mortars and grain-graters. During the Neolithic period the people of Armenia not only harvested wheat with the use of sickles but also pulled out entire plants or spikes by hand. According to archaeological data, wheat-barley mixtures are often found in Armenia. Even in the supposedly 'pure' barley material, wheat grains were found. Whether or not they were contaminants or were put there on purpose is not certain.

Tumanyan's research of archaeological materials at the beginning of the Bronze Age did not include separate remains of wheat and barley. But in material from the Urartu period (about 1000 years BC) their differentiation process was completed and pure plantings of both these crops appeared. However, it is necessary to stress that 'appeared' does not mean that wheat and barley were planted separately at all places. Tumanyan (1944) emphasized that grain material from only some regions of Karmir Blur (Araratian lowland) is characterized by purity and absence of weed seeds.

The residences of ancient Armenian (Urartu) kings were centers where substantial stocks of farm produce were concentrated or stored. The grains were cleaned before storage. In addition, 'pure' wheat and barley were planted on special fields of the kingdom. There is more information in the literature about these 'pure' plantings. For example, the chief scribe of Assyrian King Sargon II, Nabu-Schalim-Shunun, mentions that during their trip (713 BC) to the region of Hayots Dzor they saw a wheat crop of the best quality (about 300 ha). About this observation Adontz (1946) believed that it was a special field of the kingdom, signifying that particular care had been taken to keep the field free of contaminants.

Even today some farmers plant spring wheat and barley together (called 'kiardika') in mountainous zones of Armenia in order to guarantee food supply. If wheat suffered from unfavorable conditions (e.g. a disease or a drought) barley would give at least some yield. However, barley was also planted exclusively for making beer.

Most barley of the Bronze Age consists of round-grained awnless multi-row forms. At the beginning of the Urartu period they became rare as they made way for new forms with elliptical grains. Two-row forms began to prevail over multi-row ones during the process of subsequent climatic changes (Tumanyan 1948).

During the Greek military campaigns in West Asia (401-400 BC) 10,000 troops passed through the rich fertile regions of the Armenian Upland. It was noted that wheat, barley, vegetables and barley beer from Armenian settlements were made available to the soldiers (Ksenofont 1951). Ksenofont's information is confirmed by archaeological evidence of brewing beer in Armenia. A brewery and beer shop from the Urartu period were discovered during excavations at Karmir Blur (Minasyan 1961).

Through morphological investigations of plant remains from excavations of ancient Vagarshapat (beginning of the 1st millennium BC) Tamamshyan (1935) came to the conclusion that the material belonged to emmer wheat (*Triticum dicoccum*). Tumanyan (1944) found that in the Urartu period some varieties (cultivars) of naked wheat were grown in Armenia. He identified them as *T. aestivum* and *T. spelta* in archaeological materials excavated from that period.

Gulkanyan (1966) investigated materials from the excavation of the town of Argishtikhinly from the Urartu period. He divided wheat grains into two groups: round-grained and oblong-grained. Round-grained wheat was identified as *T. sphaerococcum* and oblong-grained as *T. aestivum* and/or *T. persicum.* He referred to some forms as *T. compactum* and others as *T. dicoccum* or *T. araraticum.*

Some general results of several investigations are given below. Characteristics of material studied are given as they were investigated (i.e. not dependent on the age of the excavation).

1. Carbonized remains of partially threshed plant mixtures from graveyards that belong to 2nd millennium BC, e.g. Gugavan village (S. Chilingaryan's excavation): The grains and seeds of the following plants were identified. (a) wheat kernels from round to elongated forms (similar to *T. aestivum, T. compactum, T. sphaerococcum*); (b) a spikelet of hulled two-grained wheat (probably *T. dicoccum*). There were two typical emmer grains in the spikelet ventrally oriented toward each other (as in emmer wheat); (c) kernels of multi-row barley (they are dominant over other barley types); (d) grains of different other species (*Agropyron, Lolium, Bromus,* etc.); (e) fruits and seeds of various weeds (*Caucalis daucoides, Polygonum convolvulus, Galium, etc.*), which can still be found growing in the same area; (f) carbonized remains of vegetative organs of other plants.

The materials found from the graves of Gugavan village are very interesting because they provide an opportunity to appreciate the planting conditions in economic and botanical terms. Threshed and semi-threshed grain material, apparently of barley, had been put in graves without chaff (straw).

2. During an excavation near the ancient fortress (Bronze Age) located on the hill to the southwest of Gegharkunik village, an ancient earthenware pot was accidently broken, disgorging cereal kernels. There were many barley kernels with small peduncles and some wheat grains too, particularly of short or round forms.

3. The archaeological material of ancient settlements of the town-fortress Argishtikhinly (Urartu period) was excavated by the archaeologist Martirosyan. Of 1160 analyzed grains only 13 were wheat kernels (about 1.3%), the rest were of barley. Wheat grains were small: length 4.5-5 mm; breadth 3-4 mm; width 2-4 mm (similar to *T. sphaerococcum* or *T. compactum*).

Barley grains found were 61% naked and 39% hulled. Also, there were bottle-shaped kernels. Spike bar segments were of different sizes (length 3.0-8.0 mm; breadth 1.0-2.0 mm;). Consequently, there were loose-ear and dense-ear forms. Some ear segments, usually short and narrow, had hair (there was comparatively dense hair around the edge of the ear bar). This could be identified as wild barley. Kernels and seeds of weeds also were observed.

4. The archaeological material from Lorut village of the Alaverdy region from the 3rd millennium BC (V. Avetisyan's excavations): Here only wheat grains were found. They were comparatively large but there were very small kernels also. Wheat grains were very similar to *T. compactum, T. sphaerococcum, T. aestivum* and some may belong to *T. spelta* since they had glumes. There were also germinated kernels. The presence of germinated kernels suggests that the material was conserved under moist conditions or was already wet before storage.

5. Archaeological material from Oshakan village of the Ashtarak region (4th and 6th centuries AD): Wheat grains were very similar to *T. aestivum* or *T. compactum.* Of 147 kernels, 120 were wheat, 9 rye and 18 sorghum.

6. The archaeological material from the ancient settlement of Metsamor in the Ararat Valley (excavations carried out by E. Khanzadian): These belong to the period of early Iron Age (end of 12th to 9th century BC). A mass of carbonized kernels of millet (*Panicum miliaceum* L.) was found, among which there were some emmer and barley kernels and wheat spikelets (*T. dicoccum* or *T. persicum*).

7. The archaeological material from Aigevan village of the Ararat region (the excavation of B.B. Piatrovskyi) is most interesting since it is represented by four samples from different layers (depths): (a) 12.5 m, (b) 10.5-11.0 m, (c) 8.7 m and (d) 8.0 m. Archaeologists estimated the sample ages as follows: (a) and (b) belong to the second half of the 3rd millennium BC, (c) to the end of the 3rd millennium BC, and (d) to the first half of the 2nd millennium BC. Barley prevailed over other crops in samples from all four layers. Wheat grains were present, once again, as mixtures (1-20%). Study of the archaeological materials suggests that during 1000 years an increase in grain size of both wheat and barley grains had taken place. Most of the more ancient grains have round forms. Naked barley prevailed in the samples of more ancient origin whereas hulled ones were more frequent in later periods.

The samples of the second half of the 3rd millennium BC are also interesting. Wheat kernels were naked but hulled ears were found too. There were two-grained spikelets. Kernels in the spikelets of adjacent flowers adjoined closely. Some kernels had an accrete upper tip of the second glume on the side of topknot making a 'heel' (see Pasternak, this volume).

Multi-row ears of barley were dominant in all samples, but there were also some two-row forms. The assumption that awned and two-row forms of barley were not found in the material from the Bronze Age is not confirmed. There were bottle-shaped barley kernels in all samples. Probably, this form had a 'horseshoe' at the base of the peduncle. There was also a specific dense-ear form with small grains which has since become extinct.

Some considerations on domestication of wheat and barley

About bottle-shaped barley

Such kernels have been observed in all samples of carbonized archaeological barley material from Armenia. Tumanyan identified two ancient species of barleys: round-grained *Hordeum antiquorum sphaerococcum* Thum. and the oblong elliptical kernels of *H. urartu* Thum. Judging from the picture he published (Tumanyan 1948) there are kernels with peduncles among both species. Peduncles are not formed under all spikelets, but only under the lateral ones. Therefore, it became obvious that *H. antiquorum sphaerococcum* and more so *H. urartu* correspond to *H. lagunculiformae* Bacht. (Bakhteyev 1956,1965). Tumanyan (1948), during his identification, did not consider peduncles. Regarding the kernel forms of *H. lagunculiformae,* Bachteyev (1956) emphasizes that they can be round-ellipsoid, ellipsoid and elongated-ellipsoid. The fossil samples sometimes have hair and a 'horseshoe' on the ear axis. It is a feature of wild *H. lagunculiformae.* The bottle-shaped barley can still be found in Armenia but only as a wild plant (Bakhteyev 1962). Ears of this barley were collected by this author in Turkmenistan in 1990.

About fossil hulless round-grained forms of wheat

In the opinion of specialists on phylogeny of polyploid wheat species, wheat evolved in the following way. Tetraploid wheat of *T. dicoccoides-type* arose as a result of a spontaneous cross between a wild one-grained wheat (with genomic formula AA) and a species of the section *Sitopsis* of the genus *Aegilops* L. (with the genome SS or BB). The round-grained wheat could not be among the tetraploid wheats since the parental forms are narrow-elongated. Tetraploid wheat (2n = 28) was crossed with another diploid species, *Ae. tauschii,* with the genomic formula DD to give rise to bread wheat (*T. aestivum*) with the genomic formula AABBDD.

Zohary (1969) observed that it was not until its cultivation reached Armenia, Transcaucasia and the Southern Caspian that plants of cultivated tetraploid wheat came into contact with the diploid donor of the D genome. Keeping in mind that this process of wheat hexaploidization took place a long time ago, scientists referred to short round-grained archaeological materials as bread wheat and, consequently, they determined that it is a hexaploid. For example, Heer (1878) referred to wheat samples of the Swiss Neolithic as *Triticum vulgare antiquorum* Heer. Flaksberger (1930) suggested that this variety be transferred to *T. compactum* Host, and named it *T. compactum antiquorum.* Kislev (1980) considered that short round-grained samples of the fossil wheat of the countries of the Near East are not hexaploids but tetraploids with a genomic formula AABB and he gave them a specific name - *Triticum parvicoccum* Kislev. In his scheme of classification the cultivated emmer *T. dicoccum* arose from wild tetraploid wheat *T. dicoccoides* (AABB) as a result of mutations and introgressive hybridization in the Mediterranean climate. *Triticum parvicoccum* with the compact ear and spherical grains arose from this species.

Conclusions

1. It is important to search for more remains of wheat and barley kernels grown in Armenia during the Stone Age.

2. The wheat-barley crop mixtures existed in Armenia in the past, though the relatively 'pure' plantings of wheat and barley were also present.

3. Both wheat and barley forms with small and round grains were found in more ancient samples. Subsequently, the oblong forms appeared and gradually dominated over other forms. This process was a result of climate changes on one hand and genetic changes on the other hand.

4. The gradual xeric changes in the climate led to the disappearance of round-grained wheat and round-grained as well as hulless barley from Armenia. The multi-row forms are grown now exclusively under the more moist conditions.

5. Bakhteyev named the 'bottle-like' cultivated barley (with a peduncle on the lateral spikelets) as *Hordeum lagunculiformae* Bakht. Tumanyan found such forms among the archaeobotanical materials in Armenia and named the round-grained forms *H. antiquorum sphaerococcum* Thum. and the forms with oblong, elliptical kernels, *H. urartu* Thum. (Tumanyan 1948). These forms now do not exist except in the wild.

6. The theory that barley of the Bronze Age was awnless should be further discussed. Ears with well-developed awns have been found.

7. The kernels and spikelets of hulless wheat similar to *T. dicoccum* (tetraploid) and *T. spelta* (hexaploid) have been found but their grains appear to be round.

8. The multi-embryonic barley and wheat with narrow ears similar to *T. persicum* have been found from the second half of the 3rd millennium BC.

9. It is necessary to preserve and document archaeobotanical material in special genebanks for further study on crop evolution.

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Extinction Threat of Wild African Gossypium species in their Center of Diversity - V. Holubec

Introduction

Cotton is one of the most important commercial crops in the world. Out of the four cultivated species - *G. arboreum, G. herbaceum, G. barbadense* and *G. hirsutum* - only the last-mentioned represents the staple crop at present. Wild ancestors and related species found in the Americas and Australia were extensively studied but little information was available on species from Africa and Arabia. Africa has the highest diversity of cotton germplasm. Native species of at least four genomic groups (A, B, E and F) are spread throughout the whole continent including the Arabian Peninsula. Their distribution was poorly documented and so the threat to their habitat was not envisaged. The objective of the present study was to: (1) map the distribution of wild species and naturalized (escaped from cultivation) landraces, and (2) assess the need for collecting and conserving them so that priorities could be established.

Material and methods

The major herbaria possessing *Gossypium* plant material, established by the former colonial powers (England, France, Belgium and Portugal) were visited and all available data were recorded in a computerized database. The identification of species was revised. The collecting sites were ascertained and their geographical coordinates were provided. The species distribution was plotted on the maps in the Miller's oblate stereographic projection in the scale 1:50 million (Miller 1953). *The Vegetation Map of Africa* was used to match the species distribution with various mapping units (White 1983). The borders of the mapping phytochoria were digitized and drawn into the distribution maps. Sprintsky and Snyder (1986) provided the algorithm applicable for computer graphics. The program and maps were generated at the Computing Center of Texas A & M University.

Results and discussion

Taxonomy of African and Arabian cotton

The taxonomy of African and Arabian cotton species with a special emphasis on wild species was reviewed. Two genera, *Gossypium* and *Gossypioides,* are included here. The genus *Gossypioides* used to be confused with *Gossypium herbaceum* because of some morphological similarities, but its chromosome number is different. The taxonomic treatment of the genus *Gossypium* as proposed by Fryxell (1979) was used with the following changes: *Gossypium herbaceum* var. *africanum* was accepted at the subspecies level as proposed by Mauer (1954). A subdivision of *G. somalense* into species *G. somalense, G. benadirense* and *G. bricchettii* was adopted as suggested by Vollesen (1987). *Gossypium trifurcatum* described by Vollesen (1987) was included in the subgenus *Gossypium.*

Simple keys for distinguishing the genera *Gossypium* and *Gossypioides* and their species of Africa and Arabia were designed and are available from the author.

Distribution of *Gossypium*

Distribution maps of species of *Gossypium* are available from the author. The maps for wild species are much more exhaustive and more accurate than that for cultigens. Generally it is possible to conclude that wild species of *Gossypium* are restricted in their distribution to the tropical belt between latitudes 20°N and 25°S. They are confined to semi-desert regions so that their distribution is disjunct with a hiatus in the Zaire and North Zambezi basins. *Gossypium longicalyx* and partly *G. herbaceum* subsp. *africanum* tend to occupy slightly more mesophytic habitats. Cultivated species that grow wild and primitive landraces are distributed throughout the tropical belt except for the high mountains. They predominantly occupy more mesophytic and humid habitats.

Priority regions for collecting of cotton germplasm

Africa and southern Arabia should be the places of first priority for collecting of germplasm of cotton. They have the greatest diversity of cotton germplasm, because Africa is believed to be a center of origin of the genus *Gossypium.* However, this region has been explored the least.

It is desirable to outline the collecting activities throughout the region of distribution to get as much genetic variability of a particular taxon as possible. Exploration should start in places of former successful collection of herbarium specimens to confirm the present occurrence. As the collector becomes familiar with the habitat, further investigation of suitable habitats will be easier. Then some expedition time should be devoted to examining the regions where the occurrence of the taxon could be expected but the taxon has not been collected yet. It is important to examine the limits of the distribution since a higher genetic variability may be expected there.

It is difficult to set up the regional priorities in Africa since exploration is desirable nearly throughout the continent. Particular attention must be drawn to the wild species. They are endangered by subsequent desertification on their 'arid limits' and by human influences (agriculture, grazing) on their 'humid limits' of distribution. This is important especially in the Sahel, but also in the Kalahari and the Namib Deserts. A similar situation may exist on the border of the coastal desert on the Somali peninsula, but data are not available.

On the basis of data from herbaria and from floristic and collector's literature, suggestions for future collecting activity of cotton germplasm in Africa, Arabia and adjacent islands were made. Special emphasis was given to the wild species. Cultivated species and species escaped from cultivation were treated separately, because their distribution is not connected with a particular phytogeographic region.

From these suggested regions for collecting, places of the first priority importance were chosen. The choice was made to include populations endangered in their habitats and to include species with very limited distribution (Box 1).

The second list of locations (Box 2) was outlined for further collecting activity. It covers all other regions of distribution of the wild species. Suggested localities were chosen to be confined to the areas of the most frequent occurrence of the wild species, places with higher concentration of the different species including cultivated, and places that are more easily accessed.

Box 1. First priority places (regions where taxon is endangered or very limited in distribution).

1. Niger, Air Mountains, and generally northern Sahel

   species: *G. anomalum, G. somalense;* endangered by desertification, only a few collections known; additional species: G. *hirsutum.*

2. Yemen, Aden region and SE coast

   species: G. *areysianum, G. incanum;* very limited in distribution, may be endangered; probably also G. *barbadense*

3. Somalia, central part

   species: *G. benadirense, G. bricchettii, G. somalense, G. stocksii, G. incanum, G. trifurcatum;* species not in cultivation and/or with limited distribution

4. Sudan, Meshra el Zerav

species: *G. longicalyx;* only one specimen last reported in 1910; additional species: *G. arboreum, G. hirsutum*

5. Somalia, Ethiopia, Kenya, frontier region, Upper Giuba

   species: *G. benadirense* (not in cultivation), *G. somalense*

6. Cape Verde Islands, Sao Antao, Sao Tiago

   species: *G. capitis-viridis,* distribution very limited, probably endangered, very rare; additional species: *G. hirsutum* and probably *G. barbadense*

Box 2. Places with higher concentration of cotton germplasm.

1. Mali, inner Niger delta east to Gao

   species: *G. anomalum, G. herbaceum, G. arboreum, G. hirsutum, G. barbadense*

2. Chad, east of Lake Chad to Lake Fittri and Ennedi Plateau

   species: *G. anomalum, G. somalense, G. herbaceum, G. arboreum, G. hirsutum*

3. Mozambique: Maputo and South Africa: Transvaal

   species: *G. herbaceum* subsp. *africanum, G. herbaceum* (cultivated), *G. hirsutum*

4. Angola/Namibia border, along the River Cunene, and Namibia: Windhoek Mountains

   species: *G. anomalum, G. triphyllum, G. herbaceum subsp. africanum* and probably *G. barbadense*

5. Madagascar

   species: *G. arboreum, G. hirsutum, G. barbadense*

6. Tropical West Africa: mainly Sierra Leone, Ghana, Benin, Nigeria

   species: *G. hirsutum, G. barbadense, G. herbaceum, G. arboreum*

7. Zaire: lower River Zaire and Cabinda and Luanda of Angola

   species: *G. barbadense, G. hirsutum* and the northern limit of *G. anomalum*

Conclusions

• Species distribution was corrected by plotting of the exact data

• Distribution of most species matches with certain phytochoria/mapping units of the *Vegetation Map of Africa*

• Wild species of *Gossypium* are confined to the tropical belt between latitudes 22°N and 25°S with hiatuses in the Zaire and North Zambezi basins

• The northern distribution of *G. anomalum* and *G. somalense* follows mostly the Sahel transition zone

• The southern distribution of *G. anomalum* follows the Karoo-Namib regional center of endemism and transitions to Kalahari and Zambezian regions north of 25° latitude.

• *G. herbaceum* subsp. *africanum* follows open *Colophospermum mopane* communities and adjacent undifferentiated woodlands in the valleys of the Limpopo and Cunene Rivers

• The southern distribution of the *G. somalense* complex is restricted to Somalia-Masai *Acacia-Commiphora* deciduous bushlands

• The African distribution of *G. stocksii* follows the Somalia-Masai semi-desert grassland

• The distribution of *G. longicalyx* is restricted to a small area in central Tanzania

• *G. incanum* occupies the coastal strip of S. Yemen; one specimen was found in the Nogal Valley, Somalia. This coincidence suggests the possibility of predicting their further distribution

• The distribution of wild species is restricted mostly to arid habitats which are generally endangered by desertification and overgrazing

- The distribution of restricted species is known from very few or only one locality

- *G. incanum* and *G. longicalyx* in germplasm collections are restricted to one sample only; other samples, if present, are duplications

- *G. benadirense, G. bricchettii* and *G. trifurcatum* are not available in germplasm collections

- There is a serious danger of extinction of all restricted species

- Collecting of all African and Arabian species should be accorded a high priority for *ex situ* conservation

- *In situ* conservation, at least of species which have a restricted habitat, should be considered on a priority basis

- A vocabulary of vernacular cotton names should make collecting and conservation more efficient.

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Part 4. Domestication of Crop Plants

Use of Historical and Archaeological Information in Lentil Improvement Today - W. Erskine

Introduction

Lentil (*Lens culinaris* Medikus) is a short-statured, annual, self-pollinating, food legume mainly grown in the Indian subcontinent, the Mediterranean region and North America. The crop is grown in dryland cereal-based rotations because of its nitrogen-fixing ability, its high-protein seeds for human consumption, and its straw, which is a valued livestock feed.

ICARDA has a global mandate for research on lentil improvement and is situated in the Near East arc, where the crop was domesticated. The temporal dimension given by the history of the spread of the lentil following domestication and the consequent selective forces give a perspective of applied evolution to plant breeding which is highly relevant to ICARDA's current role in any new 'spread' of the crop.

Lentil origins

The putative progenitor of the cultivated lentil is *Lens culinaris* subsp. *orientalis* (Boiss.) Ponert which is distributed from Greece in the west to Uzbekistan in the east, and from the Crimean Peninsula in the north to Jordan in the south (Ladizinsky 1979, Cubero 1981). The oldest carbonized remains of lentil are from Franchthi cave in Greece dated to 11,000 BC and from Tell Mureybit in Syria dated 8500-7500 BC (van Zeist in Zohary 1972; Hansen and Renfrew 1978). But as it is not possible to differentiate wild from cultivated small-seeded lentil, the state of domestication of these and other carbonized remains in the aceramic farming villages in the 7th millennium BC in the Near East arc is unknown. The finding of a large hoard of lentil (about 1.4 million seeds) at Yiftah-el dated to 6800 BC is, however, suggestive of domestication (Garfinkel *et al.* in Zohary 1992). The oldest find of lentil seeds that are larger than wild seeds, and therefore unequivocally domesticated (Helbaek 1969), was at Tepe Sabz, Iran; they have been dated to 5500-5000 BC. The overlap in the distribution of wild lentil and the early archaeological record indicates that lentil was domesticated in the Near East arc.

Spread

From these beginnings the crop spread to the Nile, and to Central Europe via the Danube. As lentils are repeatedly found in the early agricultural settlements of the 5th millennium BC in Europe, situated outside the distribution of *L. culinaris* subsp. *orientalis,* this is indicative of earlier domestication. Lentils were definitely associated with the start of the 'agricultural revolution' in the Old World, which was initiated by the domestication of einkorn and emmer wheats, barley, pea, flax and lentil (Zohary 1976). The crop was part of the assemblage of Near Eastern grain crops introduced to Ethiopia by the invaders of the Hamites. From the Bronze Age onward, maintained itself as an important companion of wheat and barley throughout the expanding realm of Mediterranean-type agriculture.

The dissemination eastward of the Near Eastern grain crops, including lentil, reached Georgia in the 5th and early 4th millennia BC. The crop appears in the archaeological record in India around 2500 BC as part of the Harappan crop assemblage. Alphonse de Candolle (1882) wrote that on linguistic grounds, "It may be supposed that the lentil was not in this country (India) before the invasion of the Sanskrit-speaking race." The invasion occurred before 2000 BC. The crop probably reached its current Old World range about 3000 years ago. It was

carried to the New World after Columbus.

Selective forces operating during spread

Our knowledge of the selective forces operating during the spread of the culture of lentil derives from an analysis of the variation found in current landrace populations from different geographic regions. Following widespread collecting and evaluation of landraces in the 1920s, Barulina (1930) classified the assembled variation into six groups (grex varietatum), each of which was geographically differentiated and also characterized by a complex of morphological characters, mainly qualitative, common within a group but differing in other groups. This type of geographic association is mirrored by variation in quantitative morphological traits (Erskine *et al.* 1989).

Such morphological characters are readily observable and consequently often the subject of human selection. Geographic differentiation between landraces also has been found for other more cryptic, ecophysiological factors, such as those resulting from selection for soil conditions and for climatic conditions, as the following examples illustrate.

Iron-deficiency symptoms are observable on some accessions of lentil grown in calcareous soil. In a germplasm collection of 3512 accessions originating from 18 countries, landraces from those Mediterranean countries where lentil originated (Syria and Turkey) exhibited Fe-deficiency symptoms only at very low frequencies (<1.5%) (Erskine *et al.* 1993). In these regions the soils are generally highly calcareous with pH >8.0, conditions known to reduce Fe availability. Those landraces exhibiting symptoms of Fe deficiency mostly originate from relatively warm climates, such as India (37.5% accessions showing Fe deficiency) and Ethiopia (30%), where the pH is generally 6.5-7.0 (Fig. 1). This arose from either the chance introduction to these regions of Fe-deficient founder populations, or selection pressure in favor of either Fe-deficient types or genes linked to Fe-deficiency.

In a survey of patterns of morphological variation in the world germplasm collection of lentil, phenology was found as the key to the adaptation of the crop on a macrogeographic scale (Erskine *et al.* 1989). To further understand phenology, the flowering responses to temperature and photoperiod of a world collection of 369 accessions from 13 major lentil-producing countries (25 randomly selected accessions per country) together with lines from the ICARDA breeding program were studied (Erskine *et al.* 1994). The distribution of country means for sensitivity to temperature and photoperiod illustrates the responses to selection for adaptation to new ecological environments following the spread of the crop from its origin (Fig. 2).

Fig. 1. Map indicating countries with a high frequency of winterhardiness (hatching) among lentil germplasm and countries with a high frequency of accessions showing iron deficiency (striped) (from Erskine 1997).
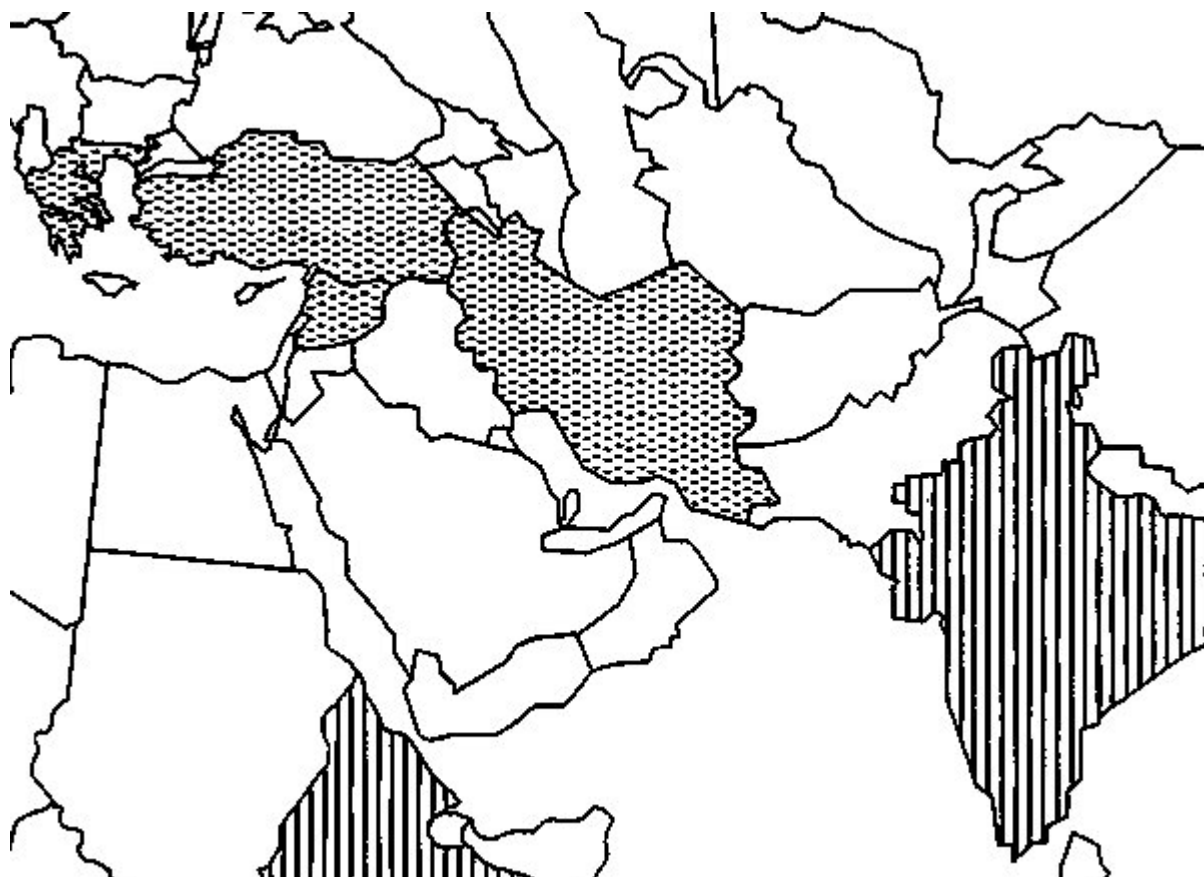
Fig. 2. Mean values for lentil accessions of different countries of origin for responses (x10^4) in flowering to temperature and photo-period. The respective means for the countries of West Asia are joined to illustrate the variation inherent in the region where the crop was domesticated. Country names are abbreviated as follows: Afg = Afghanistan, Chl = Chile, Egy = Egypt, Eth = Ethiopia, Grc = Greece, Ind = India, Irn = Iran, Jor = Jordan, Leb = Lebanon, Pak = Pakistan, Syr = Syria, Tur = Turkey, Rus = Russia (ICA represents ICARDA selections) (from Erskine *et al*. 1994).
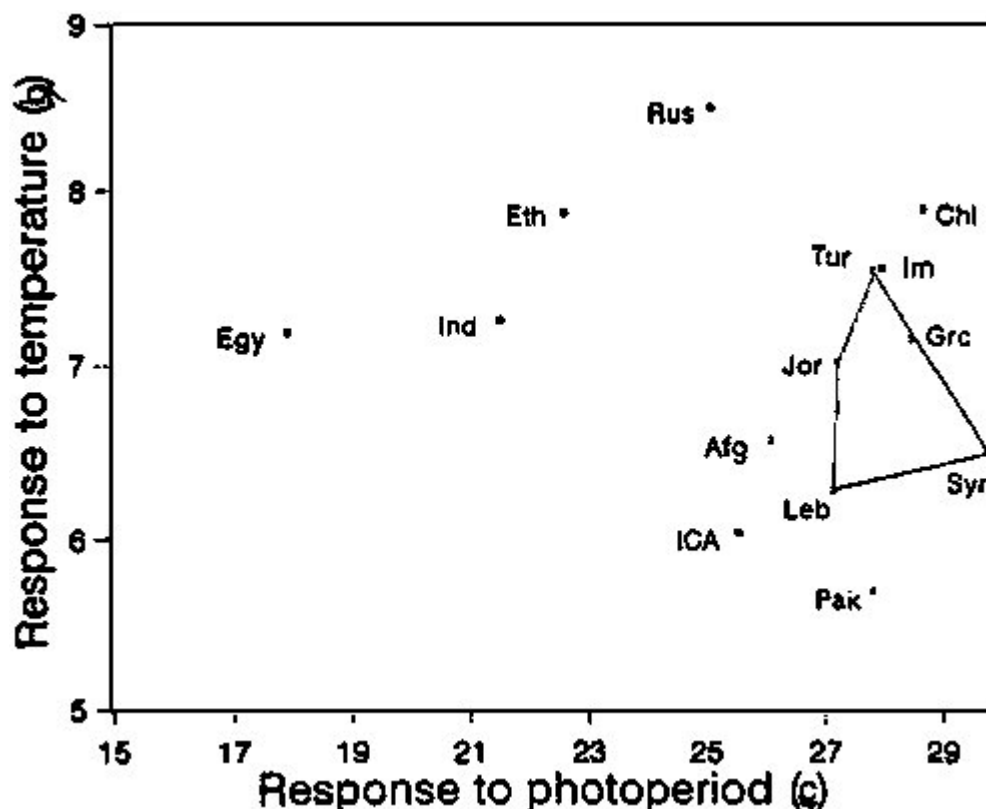
Dissemination to lower latitudes such as into Egypt, Ethiopia and India was accompanied by a reduction in photoperiodic response. Obligate photoperiodic control of the onset of flowering ensures that flowering starts annually in the same calendar period, irrespective of fluctuations in temperature. Consequently, selection against photoperiodic control in a long-day plant such as lentil implies an adaptation to relatively short days, which occur at low latitudes and which would otherwise delay flowering to an unacceptable extent. Under these conditions, the crop relies rather more on temperature than photoperiod to ensure that flowering occurs at an ecologically and agronomically appropriate time. There was also evidence that flowering in the subtropical group is more temperature-sensitive than in West Asian germplasm, on average.

Movement from West Asia to higher latitudes, for example to Russia, resulted in a modest reduction in photoperiod sensitivity and an increase in temperature sensitivity, probably reflecting the change in sowing date from winter to spring.

Temperature sensitivity to processes other than flowering, such as the base temperature for rate of germination (T_b), also has been altered during dissemination from the Near East to environments with higher temperature regimes. The mean T_b of 15 randomly selected accessions from Ethiopia and India was higher than that of similar samples from Lebanon and Turkey (Ellis and Hong 1995).

The degree of winterhardiness also has been affected in the spread of the lentil from its origins as a winter-sown crop in the Near East. A world collection of 3910 accessions was screened for winterhardiness near Ankara, Turkey, in the winter of 1979/80, when temperatures dropped to a low of -26.8°C and there were 47 days of snow cover (Erskine *et al.* 1981). In total, 238 accessions were undamaged by the cold winter. Their origins were mostly from Chile (frequency of winterhardy accessions was 28%), Greece (33%), Syria (33%) and Turkey (15%), where selection for winterhardiness had occurred through winter sowing (Fig. 1), although lentil production is found in countries farther north, where the winter is colder, such as Russia (5%), and Hungary (4%), where sowing is exclusively done in spring. The frequency of winterhardy accessions from countries with warmer winter environments, such as Egypt, Ethiopia, India and Pakistan, was <1%.

Isozyme data of the locus *aat-p* from the world collection show differences among countries and regions in the frequency of alleles and the extent of polymorphism, reflecting adaptation to local conditions (Skibinski *et al.* 1984). There is evidence that a low frequency of *Aat-p^F* is associated with the spread into South Asia, whereas a higher frequency of *Aat-p^F* is characteristic of northern European material.

Such regional differences result from the spread of the crop to new physical environments with the consequent natural and artificial selection for local adaptation. To summarize with an extreme example, the spread of lentil from the Near East into India resulted in a loss of winterhardiness and the ability to extract iron from calcareous, high-pH soils, a reduction in photoperiodic sensitivity for flowering, increased intrinsic earliness in flowering, an increase in temperature sensitivity for flowering, and in the base temperature for rate of germination. This list of factors affecting adaptation is not exhaustive. Each factor individually may be of minor importance, but collectively they illustrate the complex of interacting ecophysiological factors that determine adaptation. Superimposed on these natural selective forces is the effect of human selection on observable morphological traits, particularly the seed, for culinary and agronomic preferences.

The *pilosae* group of the Indian subcontinent is also characterized by two endemic qualitative morphological traits: precocity in flowering and maturity, and a low biomass. Furthermore, lentil germplasm from India is among the least variable among lentil-producing countries, despite India being the largest lentil-producing country in the world. Recent evidence from isozyme (7 loci) and random amplified polymorphic DNA (RAPD) (22 loci) analysis indicates a similar striking difference between germplasm from South Asia and that from the rest of the world; additionally South Asian germplasm was found low in diversity (Ferguson *et al.* 1998). These data confirm the morphological and physiological distinctiveness of *pilosae* germplasm. The simplest explanation has the introduction around 2000 BC of a founder population adapted to the new environment that was probably both small in number and low in variability which resulted in a genetic bottleneck in South Asia (Erskine *et al.*, unpublished). This still limits breeders' progress today. Indeed, a reconstruction of the phenological problems associated with the initial spread of the crop into the Indo-Gangetic Plain was inadvertently made with the introduction into that region of lentil selected in West Asia through ICARDA international nurseries in its early years (Ceccarelli *et al.* 1994). Lentil selected in West Asia, when sown in India and Pakistan, mostly came into flower as the indigenous lentils were maturing.

Use of information in breeding

Armed with an understanding of the specific adaptation of lentil, the local constraints to production and the various consumer requirements of different geographic areas for seed, the breeding program at ICARDA aims to produce genetic material suitable for national cooperators. The program has been designed as a series of separate, but finely targeted streams linked closely to national breeding programs (Ceccarelli *et al.* 1994) (Table 1). As we have seen, many of the selective forces important in the adaptation of the crop are environment-specific, such as temperature and photoperiodic sensitivities. Clearly, selection undertaken in conditions very different from those in the target environment will have a lower response in the target environment than selection conducted directly within the target environment. Harnessing the specific comparative research advantages of ICARDA and its national program partners, crosses (previously agreed with cooperators) are made and segregating generations advanced at ICARDA. The selection of bulk segregating populations is undertaken in the target environment by national programs. Since 1985, we have made specific crosses for national programs, for example, Algeria, Bangladesh, Egypt, India, Jordan, Morocco, Nepal, Syria and Turkey. Details may be found in ICARDA (1995).

We have made a major effort to widen the genetic base in the Indian subcontinent using three approaches, namely plant introduction, hybridization and mutation breeding. As mentioned above, plant introductions from West Asia flower as indigenous material matures in the Indian subcontinent. The asynchrony in flowering has isolated *pilosae* lentils reproductively. However, the introduction of ILL 4605, an early flowering, large-seeded line, has resulted in its release as 'Manserha 89' for wetter areas of Pakistan and its widespread use as a parent in breeding programs in the region. Hybridization between *pilosae* and exotic germplasm, primarily at ICARDA, followed by selection in the Indian subcontinent has resulted in cultivars with improved disease resistance and yield in Bangladesh and Pakistan. Mutation breeding has given new morphological markers and several promising lines.

Table 1. Target agro-ecological regions of production of lentil and key breeding aims.

Region	Key traits for recombination
Mediterranean low to medium elevation	
300–400 mm annual rainfall	Biomass (seed + straw), attributes for mechanical harvest and wilt resistance
<300 mm annual rainfall	Biomass, drought escape through earliness

Morocco	Biomass, attributes for mechanical harvest and rust resistance
Egypt	Seed yield, response to irrigation, earliness and wilt resistance
High elevation	
Anatolian highlands	Biomass and winterhardiness
N. African highlands	Seed yield and low level of winter hardiness
South Asia and E. Africa	
India, Pakistan, Nepal, Ethiopia	Seed yield, early maturity and resistance to rust, ascochyta and wilt
Bangladesh	Seed yield, extra earliness and resistance to rust and *Stemphylium*

The example of the widening of the genetic base of the lentil in South Asia illustrates the value of the historical perspective in plant improvement. Although ICARDA and its national program partners are undertaking the first systematic lentil improvement program with access to a wide range of genetic diversity and modern biotechnological tools, the efficiency of this research has been increased by an awareness that we belong to the approximately 200th generation of cultivators/selectors who have grown the crop since its domestication.

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What Can Molecular Markers Tell Us about the Process of Domestication in Common Bean? - Paul Gepts

Introduction

Alphonse de Candolle, the founder of the study of crop evolution, was primarily interested in biogeography, the study of distribution of plants in relation to their environment. In his opinion, among the factors influencing this distribution are 'historic' factors such as glaciation events that are not related to the intrinsic adaptation characteristics of the species. When he considered crop plants, he posited that one particular historic event - domestication - had had a paramount importance in determining their adaptation and, hence, distribution, as well as their genetic characteristics (de Candolle 1882).

Four types of evidence could be utilized to determine the origin of domestication of crop plants according to de Candolle (1882). These were archaeological (or more specifically archaeobotany), botanical (i.e. the distribution of the wild, ancestral relative), historical (or the existence of a written record documenting the existence or importance of the crop) and linguistic evidence (i.e. the existence of words designating the crop or objects or concepts related to the crop in native languages). Of these four types, the first two provide the most abundant and reliable evidence (Harlan and de Wet 1971). Since the time of de Candolle, however, additional scientific methods have increased considerably our power to determine centers of crop domestication based on archaeological and botanical arguments (Smith 1995).

Although common bean is not a species originating in the Near East, the focus of the present symposium, it presents nevertheless an interesting domestication history, which is only recently being elucidated. The first botanically accurate description of common bean in European herbals dates from 1542. Whereas barely 50 years had passed after the conquest of the Americas, the actual origin of the crop had already been lost to the writer of the herbal and later European botanists. Linnaeus assigned the origin of common bean to India; de Candolle (1882) himself expressed doubts that common bean had been domesticated in the Americas. It was only during and after the Second World War that it became generally admitted that common bean originated in the Americas. The conclusion was based on the discovery of wild common bean in Argentina (Burkart and Brücher 1953) and Guatemala (McBryde 1947) and archaeological remains in the Americas (Kaplan and Kaplan 1988).

Based on the extensive distribution of the wild relative (Fig. 1), Heiser (1965) and Harlan (1975) speculated that common bean originated through multiple domestications as did other crops originating in the Americas, such as cotton, pepper and amaranth. In the variability present in the Cambridge (UK) collection, Evans (1976) also observed that there was a Mesoamerican cultivar group with smaller seeds and an Andean group with larger seeds. None of these observations, however, provided substantial experimental evidence and hence a clearer picture of the actual process of domestication for this species. For example, one could ask whether the two cultivated groups identified by Evans (1976) resulted from distinct domestications or a single domestication event followed by divergence into a small-seeded and a large-seeded group. One could also ask where these single or multiple domestications took place.

The archaeological record of the origins of agriculture in the Americas is rather limited. In Mesoamerica, there are only five major sites. This important type of information therefore pales in comparison with what is available in the Near East (Zohary and Hopf 1993). In part, this may be due to the relatively humid environment required by many crop relatives in the Americas, which render long-term conservation of crop remains less likely. Therefore, in relative terms compared with archaeological information, there is a relatively higher emphasis on botanical evidence to decipher crop evolution in the Americas than in the Near East.

In this chapter, I would like to show how the use of molecular marker information has increased our understanding of the domestication process in common bean (*Phaseolus vulgaris* L.), a crop originating in the Americas. In addition, I hope to demonstrate how molecular analyses can bridge the gap that has separated botanical and archaeological evidence, the twin pillars on which rests the study of crop evolution. The power of molecular biology to change scientific paradigms is by no means unique to this field but extends to many other

fields as well.

Once upon a time there was a bean...

General methodological principles

Our current understanding of the origins of domestication in common bean is based on a two-pronged approach relying on the study of wild-growing *P. vulgaris* beans, on one hand, and the use of biochemical or molecular markers, on the other. The use of wild beans is predicated on the fact that their dispersal occurs over much smaller distances (at most a few meters after each vegetation cycle, if at all) than their domesticated descendants. The latter are subject to long-distance exchange, trade, gift or human migration, all of which tend to obscure the original geographic distribution patterns of genetic diversity. A prerequisite for such an approach is of course the availability of wild germplasm. Recent explorations have provided a more complete representation of the actual distribution of wild *P. vulgaris* (Fig. 1) (Debouck *et al.* 1993; Freyre *et al.* 1996; Beebe *et al.* 1997). Wild beans are distributed from approximately 30°N Lat. to 30°S Lat. at mid-elevations from 1000-2500 m asl in regions with moderate rainfall. A common characteristic of the environments in which wild beans are found is the existence of a marked dry season, an important feature needed for seed dispersal.

Genetic relatedness is traditionally assessed with morphological phenotypic traits. Plants with a similar phenotype are inferred to be genetically related either through common ancestry or through geneflow (hybridization). Occasionally, however, inferences based on phenotypic similarity are erroneous. Plants can arise from different selection episodes leading to the same phenotype (convergent evolution). In addition, similar phenotypes can have a different genetic basis (genetic heterogeneity). In both cases, an inference of genetic relatedness would be unwarranted. In contrast, biochemical, and even more so, molecular markers provide information on genetic relatedness that is generally (although not always) devoid of selective influences.

Fig. 1. Distribution of the three major genepools of wild *Phaseolus vulgaris* L. in Latin America.

Not all biochemical and molecular markers were created equal! Differences have been observed with regard to the ease of analysis, reproducibility, level of polymorphism, number and genome distribution of loci (Rafalski and Tingey 1993). Of particular note is the molecular basis of polymorphisms. The more complex the basis, the more desirable the marker, because complexity will reduce the probability of repeat mutations, especially in conspecific materials, which are, by definition, closely related. For example, polymorphisms based on DNA nucleotide substitutions are simple changes that could presumably occur repeatedly. Analyses based on single or few RAPD or RFLP markers are therefore unreliable in determining genetic relatedness (Skroch *et al.* 1992). Conversely, analyses that sample a large number of changes at the molecular level, because they include either a large number of markers or complex markers such as actual DNA sequences or multigene families, are more robust with regard to repeated changes. For example, banding patterns of seed proteins such as phaseolin in common bean, when analyzed in denaturing SDS-polyacrylamide gel electrophoresis, represent a composite image resulting from changes at the DNA nucleotide level (duplication of genes, within-gene duplications, nucleotide substitutions) and at the translation level (co - and post-translational modifications). Therefore each pattern is unlikely to have arisen more than once. As a consequence, genotypes that exhibit the same protein pattern are likely to share a common ancestor (Gepts 1988).

One of the major experimental difficulties in crop evolutionary studies is the distinction one has to make between ancestry (domestication) and geneflow as a cause of genetic relatedness. This is particularly the case given that wild ancestors and domesticated descendants belong to the same biological species and can therefore freely hybridize. Hence, similarity between ancestors and descendants even at the molecular level cannot be assumed to be due to domestication without additional data. For example, DNA sequence data and the utilization of an outgroup (e.g. closely related species) can shed additional light on this problem because they can provide information on the nature of the polymorphism and the direction of the change, i.e. the ancestral vs. descendant states of the molecular polymorphism. This will be illustrated below with the case of phaseolin.

Domestication pattern

The origin of the *Phaseolus vulgaris* progenitor in its wild state can be traced to the Pacific slope of Ecuador and northern Peru, based on the distribution pattern of direct repeats in phaseolin seed protein genes (Kami *et al.* 1995). Phaseolin is coded by a small multigene family inherited as a single Mendelian unit and located on linkage group B7 (Brown *et al.* 1981; Nodari *et al.* 1993). The phaseolin locus is at most 190 Kb long (Llaca and Gepts 1996) and contains 6 to 9 genes (Talbot *et al.* 1984). Differences among these phaseolin sequences include nucleotide substitutions and the presence or absence of tandem direct repeats. Three repeats have been identified so far: a 21 bp repeat in the third intron, a 15 bp repeat in the fourth exon and a 27 bp repeat in the sixth exon.

The existence of these tandem repeats provides an interesting landmark to follow the evolution of phaseolin genes. Indeed, the generation of a repeat is a more likely event than the precise loss of such a repeat, which would be needed to restore a sequence without repeats. Hence, phaseolin genes without repeats represent probably a more ancestral state than phaseolin genes with repeats. This was verified by analyzing the presence of tandem repeats with a polymerase chain reaction (PCR) test of phaseolin sequences in two subspecies of a related species, *P. coccineus* subsp. *polyanthus* and *P. coccineus* subsp. *coccineus.* In these two taxa, none of the three repeats could be identified, suggesting that the repeatless state is indeed the ancestral state.

A survey was then conducted among wild *P. vulgaris* to determine if any phaseolin haplotypes lacked genes with tandem repeats. Only wild bean populations from Ecuador and northern Peru on the Pacific slope of the Andes appeared to be devoid of phaseolin genes with tandem repeats (Fig. 2; Kami *et al.* 1995). It was inferred that these wild populations therefore represent the presumed ancestor of the species. This conclusion is somewhat unexpected as most wild *Phaseolus* species are distributed in Mexico. One could have thought that *P. vulgaris* would have originated in that region as well and that other wild *P. vulgaris* populations distributed elsewhere were ultimately derived from Mexican ancestors. It may be, however, that some wild *Phaseolus* ancestors ('proto-vulgaris' and other species) were dispersed from Mexico to Central America and the Andes to give rise to locally distributed wild *Phaseolus* species, such as *P. costaricensis* (Freytag and Debouck 1996) and *P. augusti* (Freyre *et al.* 1996). From such a local distribution, a species such as *P. vulgaris* could have acquired a secondary, broader distribution by dispersal toward the north and south (see below). It is worth remembering that lima bean (*P. lunatus*) also shows an extensive distribution of its wild relative from Mexico to Argentina and that the species consists of two genepools, an Andean genepool originating on the Pacific side of the Andes in Ecuador and northern Peru (although at lower altitudes than wild *P. vulgaris*) and a 'Mesoamerican' genepool distributed from Mexico to the southern Andes. Although the domestication region of the 'Mesoamerican' genepool is unknown so far, it is likely to be located somewhere in Mesoamerica, given that most Mesoamerican cultivars are located there (Salgado *et al.* 1995).

Fig. 2. Polymerase chain reaction amplification of part of the phaseolin genes surrounding the 15 repeat. 1: T phaseolin (Andean); 2: S phaseolin (Mesoamerican); 3: I phaseolin (Ecuador and northern Peru). Adapted from Kami *et al.* (1995).

From the small nuclear area in Ecuador and northern Peru, wild *P. vulgaris* were dispersed toward both the north (Colombia and Venezuela, Central America and Mexico) and the south (southern Peru, Bolivia and Argentina) to achieve their current distribution (Fig. 1). In a subsequent step, multiple domestications took place in the Mesoamerican and Andean regions. At least one domestication may have taken place in west-central Mexico (Jalisco), a conclusion based on phaseolin data. Most Mesoamerican cultivars exhibit the same phaseolin type ('S'-type). Wild beans with the same phaseolin type and without morphological signs of past hybridizations to domesticated beans are concentrated in the Mexican state of Jalisco, suggestive of a possible domestication site in that area (Gepts 1988). Interestingly, Doebley *et al.* (1984) suggested a similar domestication area for maize.

A second major domestication took place in the southern Andes although a more specific region awaits confirmatory data. Phaseolin data suggest possible multiple domestications within the Andean region because at least four phaseolin types have been identified among Andean beans. Alternatively, the original populations that were domesticated were polymorphic for phaseolin. Further data are needed to distinguish between these possibilities. A third, likely minor domestication may have taken place in Colombia, although regions in Central America deserve further study because samples of wild *P. vulgaris* from that area were unavailable.

Issues raised by these observations

1. Molecular analyses appear to allow us to locate more precisely the centers of origin and domestication. It remains to be determined, however, if these results can be confirmed with further analyses of additional markers and plant materials.

2. Data from several crops mutually can potentially reinforce the identification of centers of domestication. When several crops appear to have been domesticated in the same well-defined area, such as maize and common bean in west-central Mexico, one can infer that several thousands of years ago, people in these areas developed the technology of domestication and agriculture and applied it to several crops simultaneously.

3. Once domestication was accomplished in a certain area for a certain crop, it may not have been attempted again within a certain distance. It is as if crops, or the people who domesticated them, had gained a competitive advantage, such that domestication was not attempted again. One can speculate as to the nature of this advantage. Perhaps the assemblage of domestication traits characterizing a crop is an unusual one and could only be reconstituted with very low probability elsewhere. Alternatively, the new agricultural societies overwhelmed other, non-agricultural societies by their increased population growth caused by sedentism and the attendant reduction in birth spacing.

4. Molecular biology provides a way of characterizing genetic diversity in archaeological remains. PCR amplification of remnant DNA sequences and sequencing of the amplification products provides a way of comparing genetic diversity in archaeological remains and contemporary plant materials. Such an analysis has been accomplished by Goloubinoff *et al.* (1993) for maize and Brown *et al.* (1994) for wheat. The probability of DNA amplification is higher with desiccated than with charred remains, although Goloubinoff *et al.* (1993) claim to have amplified DNA from charred remains too.

Post-domestication divergence

Common bean is perhaps best known for the high level of phenotypic diversity, particularly for seed type (color, color pattern, size and shape). This broad diversity is a consequence of the wide range of cultural environments under which common bean is grown, both in the Americas and elsewhere. This diversity has made it difficult to recognize patterns of genetic diversity in the domesticated genepool because of the possibility of convergent and reticulated evolution.

Analyses of biochemical traits such as isozymes and phaseolin seed protein have provided additional information on this problem. Koenig and Gepts (1989) and Singh *et al.* (1991a) analyzed isozyme diversity in wild and domesticated germplasm, respectively. From these studies, it was possible to identify clusters of cultivars within the Andean and Mesoamerican genepools that shared a common isozyme allele. Further analyses of phenotypic diversity were conducted with multivariate statistical analyses (canonical and discriminate analyses) (Singh *et al.* 1991b). Results showed that the isozyme clusters could also be distinguished by morphological, agronomic and ecological traits. For example, in the Mesoamerican genepool, three subdivisions or races can be distinguished (Singh *et al.* 1991b, 1991c). Race Mesoamerica represents cultivars originating predominantly from the warmer, more humid areas of Mexico, Central America and Colombia. Possibly, this race could be split further to account for an additional, minor domestication area in Central America or Colombia (the 'B' phaseolin cultivars, Gepts and Bliss 1986). Race Durango includes cultivars from the northern highlands of Mexico, which have a cooler, more arid environment. Race Jalisco consists of the most traditional common bean cultivars, originating predominantly in the humid central and southern highlands of Mexico. A similar subdivision in three ecogeographical races has been established for the Andean genepool (Singh *et al.* 1991b, 1991c).

Figure 3 summarizes the current status of the domestication scenario in common bean. The question marks refer to the racial diversification process (see below). The arrows indicate rare cases of geneflow between the two major genepools.

Fig. 3. Current domestication scenario in common bean. The question marks refer to the current lack of data regarding the actual pattern of domestication within the Andean and Mesoamerican regions. The arrows at the top of the figure indicate rare instances of geneflow between the Mesoamerican and Andean domesticated genepools.

Issues raised by these observations

1. One question arising from these observations is the cause of this racial diversification. In the Mesoamerican genepool, phaseolin data suggest a single domestication event because the domesticated genepool contains only one phaseolin electrophoretic type compared with over 15 in the corresponding wild genepool (Gepts *et al.* 1986). This suggests that racial diversification in the Mesoamerican genepool cannot be attributed to separate domestications but to events subsequent to domestication. One possibility is the existence of geneflow from wild to domesticated bean populations. As domesticated beans were disseminated from their presumed center of domestication in Jalisco, Mexico, they may have been subjected to geneflow from wild populations in other regions of Mexico. An AFLP diversity study of wild and domesticated common bean from Mexico does not appear to support this possibility as most domesticated beans are located in a distinct cluster from the wild beans. In turn, these observations suggest that racial diversification in the Mesoamerican genepool may have taken place as a consequence of selection of genetic diversity within geographically isolated populations after dispersal from the center of domestication. In the Andean genepool, phaseolin data (Gepts *et al.* 1986) suggest a multiple domestication pattern or, alternatively, domestication from a phaseolin-diverse wild population. Data are currently lacking to determine a possible role for geneflow in the Andean genepool.

2. If racial diversification in the Mesoamerican genepool involved selection after dispersal to other ecogeographic regions of Mexico and Central America, then it should be interesting to attempt to trace ancient human migrations in Mexico, which may be associated with the spread of agriculture and crops. Such a study would be very similar to the ones performed by Ammerman and Cavalli-Sforza (1984) and Sokal *et al.* (1991). In these studies they identify gradients of gene frequencies among contemporary European populations, the most important of which is a SE-NW gradient, which, the authors claim, stems from the introduction of agriculture from the Near East into Europe via diffusion.

What does it take to get a domesticated bean?

Wild relatives and their crop descendants show marked phenotypic differences, collectively called the domestication syndrome (Hammer 1984). As a consequence, they have been classified in different taxonomic species, which is unjustified given that often they can be freely crossed. Based on the traditional neo-Darwinian theory of evolution, one would expect that these marked phenotypic differences would be controlled by a large number of genes, each with a small phenotypic effect. This view reflects a view of evolution involving very gradual changes in environment and adaptation. This may not have been the case during domestication (nor in natural environments for that matter) where the domesticated and natural environments are quite different. Hence, adaptation to cultivation represented selection for a radically different environment over a time scale that would have been very short in an evolutionary context (even a few 100 generations should be considered a very short period in evolution). This suggested that major genes might have played a role during domestication because only such genes would have provided a fast response to the rapidly changing environment imposed by cultivation.

To test this view of evolution during domestication, an experiment was conducted to determine the inheritance of the domestication syndrome in common bean (Koinange *et al.* 1996). A recombinant inbred population was established from a cross between 'Midas' (a snapbean cultivar representing the 'ultimate' in bean domestication) and 'G12873' (a wild bean from Mexico). In this RI population, a linkage map was constructed with RFLP markers regularly spaced throughout the genome. In turn, this map was used to conduct a quantitative trait locus (QTL) analysis for quantitative traits and to map major genes involved in the domestication syndrome. The following traits were studied.

Pod dehiscence

The onset of the dry season coincides with the maturation phase of the life cycle of wild beans. During the progressive desiccation of the plant, fibers located in the pod walls and sutures shorten and, hence, cause the explosive dehiscence of the pods. (Without desiccation during the dry season, pods rarely open and seeds germinate in the pods, causing a marked reduction in fitness.) Pods of domesticated beans contain fewer or no fibers and therefore do not open at maturity. This difference in the capability of seed dispersal is one of the most important characteristics distinguishing wild and domesticated wild beans. It can be easily recognized in dry pod remains: dried wild pods are strongly twisted (owing to the oblique orientation of fibers in the pod walls), whereas dried domesticated pods are not or only slightly twisted. Presence or absence of fibers is controlled by the *St* gene.

Seed dormancy

Because the onset of the growing (wet) season is irregular, plants have adopted seed-dormancy mechanisms to insure against premature germination during the first rains. In common bean, dormancy is essentially impermeability of the seed coat, which prevents immediate imbibition of the seed. Prior to this study, no studies had ever been undertaken about the inheritance of dormancy in common bean.

Growth habit

Wild beans are viny plants that use shrubs or trees as support. During common bean evolution, there has been a selection for a bush growth habit. Growth habit consists of several subtraits, including the number of nodes and pods on the main stem, the length of the internodes, and type of stem termination (vegetative or indeterminate vs. reproductive or determinate). The latter traits are conditioned by the *fin* gene.

Photoperiod sensitivity

Photoperiod sensitivity plays a crucial role in scheduling of flowering, such that maturation will take place at the beginning of the dry season. Earlier maturation will result in reduced or lack of seed dispersal. Later maturation will prevent sufficient development of seeds before the dry season sets in. Common bean, having originated in the tropics, is a short-day (long-night) plant, which will flower only under daylengths of 12 hours or less. During dispersal from centers of domestication, dayleingth neutrality was selected, whereby common bean plants will flower under any daylength. Photoperiod sensitivity is controlled by the *Ppd* gene.

Seed size and color

Selection by farmers and consumers has led to larger pods and seeds with different colors, among them white (absence of pigmentation) conditioned by the *p* gene.

Four conclusions were drawn from the results. First, for many traits it was possible to identify major genes. For example, at least four genes controlled seed dormancy, one of which accounted for at least 50% of the

phenotypic variation. Second, for most of the traits, more than 50% of the phenotypic variation could be accounted for in genetic terms, suggesting that heritability of most traits was high. Third, distribution of genes involved in the domestication syndrome appeared to be non-random, as there was a relatively higher concentration of genes on linkage groups 1, 2 and 7. Linkage group 1 appeared to be particularly important because it included genes for photoperiod (*Ppd*), determinacy (*fin*) and internode length.

Issues raised by these observations

1. The genetic control of the domestication syndrome in common bean, which is actually quite similar to the one observed in maize (Doebley and Steck 1991), reflects the process of domestication in that we observe major genes and high heritability for most traits. If farmers practised conscious selection, mutations with major effect would have been more easily detected than minor ones. Even in the case of unconscious selection, adaptation to the cultivated environment would have been more rapid with these major mutations. In addition, highly heritable traits would also have been more amenable to selection, especially in variable environments. Finally, the concentration of many genes for domestication in a limited number of genomic regions would have facilitated recovery of domesticated types after outcrossing between wild and incipient domesticates.

2. Given the simple genetic control of the domestication syndrome, domestication could have proceeded rapidly. There are at least two caveats for this statement:

> • We have in many cases little information about the actual selection pressure that was applied during domestication. Archaeobotanical sequences encompassing wild to domesticated materials could help shed light on this problem.

> • Arguments about speed of domestication are generally based on single traits (e.g. Hillman and Davies 1990). How long did it take, however, to assemble the domestication syndrome? It is unlikely that all mutations necessary for the domestication syndrome occurred in a single plant. This suggests that hybridization and recombination took place. However, many crops are predominantly self-pollinated. This reproductive mode would have slowed down the recombination among mutant genotypes compared with allogamous plants. Again, a sequence from wild to domesticated plants including different types of organs would be very useful.

Conclusion

Molecular biology methods can provide a bridge between the main study fields of crop evolution - archaeobotany and plant science - by providing information on putative centers of domestication, potential identification of plant (and human) migration patterns from the center of domestication, the time frame for the domestication process, and a molecular characterization of archaeological remains. Thus, by analogy with the Tigris and Euphrates Rivers of the Fertile Crescent, which after having flowed separately for most of their courses are finally united before they reach the sea, a closer association of these two fields can be achieved using molecular biology as a unifying tool.

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On the Origin and In Statu Nascendi Domestication of Rye and Barley: A Review - V. Jaaska

Introduction

The crucial difference between cultivated cereal crops and their wild relatives is in ear fragility at maturity. Easy shattering of spikes into spikelets upon maturity is essential for seed dispersal and survival in the wild, whereas forms with non-brittle ears survive only under cultivation. It is generally assumed that most Triticeae crops have been domesticated from their wild relatives by selection of non-shattering individuals which sporadically appear in wild populations as rare mutants (Zohary and Hopf 1993). However, there are no documented cases of the appearance of non-brittle mutants in wild populations, except observations of introduction from cultivars into weedy forms. The appearance of non-brittle mutants seems to be a rare event which may be induced under specific conditions.

Interspecific hybridization may activate transposition of mobile genetic elements which may be one potential source of increased mutation rates. A hypothesis was proposed that rye and wheat forms with varying ear fragility may have arisen as a result of interspecific hybridization processes between different wild species (Jaaska 1975). Taking into account that non-brittle mutants will persist in the wild only for a limited number of generations after their appearance, it follows that rye and barley should have been domesticated *in statu nascendi* from the ancient hybrid populations of their wild relatives.

Rye

Despite considerable disagreement among taxonomists about the delimitation of rye species and their intraspecific taxa (Kobyljanskij 1975; Gandilyan 1976; Hammer *et al.* 1987) the rye genus *Secale* L. may be treated as consisting of three valid biological species (Sencer and Hawkes 1980; Jaaska 1975,1983):

- The outcrossing annual *Secale cereale* L. s.l, including the European cultivated rye (subsp. *cereale*), the Transcaucasian cultivated and weedy rye with a tough rachis (subsp. *segetale* Zhuk.), and various weedy and wild forms of the annual self-incompatible rye with a brittle rachis such as subsp. *ancestrale* Zhuk. s.l, including weedy subsp, *ancestrale* Zhuk. s.str, weedy subsp. *afghanicum* (Vav.) Hammer, weedy subsp. *dighoricum* Vav., and wild subsp. *vavilovii* (Grossh.) Kobyl. s.str., non s.l. of Kobyljanskij (1975).

- The outcrossing perennial *Secale strictum* Presl., syn. *S. montanum* Guss., with several subspecies: subsp. *strictum* (= *S. dalmaticum* Vis.), subsp. *anatolicum* (Boiss.) Hammer, subsp. *kuprijanovii* (Grossh.) Hammer, subsp. *ciliatoglume* (Boiss.) Hammer, and subsp. *africanum* (Stapf) Hammer.

- *Secale sylvestre* Host. - a cleistogamous annual of sandy dunes and coasts.

A cleistogamous annual, originally collected by Kuckuck in Iran and attributed to *S. vavilovii* (Kuckuck and Kranz 1957), may deserve a specific rank as *S. iranicum* Kobyl., syn. *S. vavilovii* Grossh. sensu Khush, non sensu Grossheim (1924) or sensu lato of Gandilyan (1976), owing to its reproductive isolation as a result of its cleistogamous breeding system. Likewise, South African endemic perennial rye may be recognized as *S. africanum* Stapf because of its autogamous breeding system.

Grossheim (1924) described *S. vavilovii* as a short-statured (stems 20-35 cm) wild annual with short (4-8 cm) fragile spikes which he collected in Nakhitshevan from a dry habitat on volcanic ash soil. Populations of short wild annual rye were later found to occur in different dry regions of Armenia by Gandilyan (1976) who attributed the short stature to a phenotypic adaptation to a dry and nutrient-poor habitat. On those grounds he proposed to treat all wild and weedy annual ryes with a brittle rachis as *S. vavilovii* s.l. separately from the cultivated *S. cereale* s.str. To give these forms a specific rank is questionable because they are not reproductively isolated from non-brittle weedy *S. cereale* subsp. *segetale.* Their inclusion under *S. cereale* subsp. *vavilovii* s.l. as proposed by Kobyljanskij (1975) contradicts the botanical nomenclature rules because of the priority of subsp. *ancestrale* Zhuk. at the subspecies level (Zhukovsky 1928).

Vavilov (1917) expressed a view that cultivated rye evolved from a wild perennial rye through the appearance of annual weedy forms which in turn were domesticated by unconscious selection of non-brittle forms under cultivation in barley and wheat fields. Later he reported finding a weedy rye in Afghanistan with fragile ears which he attributed to *S. cereale* var. *afghanicum* and proposed that it might be an initial form from which semi-brittle and non-brittle forms of weedy rye were spontaneously selected under cultivation in wheat and barley fields in northern areas and higher altitudes (Vavilov 1926). He also further argued that *S. cereale* may have evolved from a perennial *S. montanum* with wild *S. vavilovii* Grossh. acting as a link between them. According to Vavilov, rye was domesticated in the Near East region as a secondary weedy crop (subsp. *segetale*) and only thereafter spread to European countries and was used as a distinct crop.

Alternatively, the present-day weedy ryes with brittle and semi-brittle rachis are products of introgressive hybridization of the cultivated non-brittle subsp. *segetale* with wild rye subsp. *vavilovii* s.str. Segregants from this hybridization acquired a weedy trait from subsp. *segetale* and became field weeds. Artificial hybrids between wild, weedy and cultivated forms of *S. cereale* are completely interfertile and show regular meiosis (Nürnberg-Krüger 1960a; Khush 1962, 1963), indicating that they comprise a single biological species.

It is generally accepted that all annual rye species have evolved from the perennial *S. strictum* (Stutz 1972; Hammer 1990). *Secale cereale* and *S. strictum* differ by two large translocations between three of the seven chromosomes, but intraspecific taxa have the same chromosome arrangement in both species (Riley 1955; Stutz 1957; Khush and Stebbins 1961). Polymorphism for reciprocal translocations has been described in populations of *S. cereale* (Candela *et al.* 1979). The evolution of *S. cereale* from *S. strictum* should thus involve fixation of two reciprocal translocations (Riley 1955; Khush and Stebbins 1961) which would be possible only by the involvement of an autogamous intermediate. Stutz (1972) suggested that cleistogamous annuals *S. sylvestre* and *S. vavilovii* sensu Khush (= *S. iranicum*) might represent intermediate stages in the evolution of *S. cereale* from *S. strictum.*

Secale sylvestre has the same chromosomal arrangement as *S. strictum,* but a low crossability with it, or differs in only a small chromosomal translocation, whereas *S. iranicum* was found to have the same chromosomal arrangement as *S. cereale* (Nürnberg-Krüger 1960b; Stutz 1972). According to these data, Stutz (1972) suggested that cleistogamous annual *S. sylvestre* has been derived from *S. strictum* and has then given rise to a similarly cleistogamous annual *S. iranicum* by fixation of two chromosomal translocations, while *S. cereale* was assumed to emerge from *S. iranicum* by acquisition of the outcrossing breeding system by introgression from *S. strictum.*

My studies of isoenzyme variability among the rye species established that *S. cereale* and *S. strictum* display partially homologous polymorphism of many isozymes with most allozymes shared between them. It may be seen from Table 1 that *S. iranicum* is fixed for one of the allozymes found in *S. cereale* and *S. strictum,* whereas *S. sylvestre* has unique allozymes of acid phosphatase ACP-B, anodal peroxidase PRX-C, and aromatic alcohol dehydrogenases AAD-A and AAD-E (Jaaska and Jaaska 1984). In the light of the isoenzyme data, it has been concluded that *S. sylvestre* is a lateral branch of evolutionary divergence form S. *strictum* and not an intermediate leading to *S. iranicum* and *S. cereale.*

Morever, *S. strictum* and *S. sylvestre* are well isolated in nature by growing in different ecological habitats and do not hybridize freely. Instead, I suggest that some unknown inbreeding form of subsp. *vavilovii* related to *S. iranicum* might be an intermediate from which both brittle- and tough-rachis forms of *S. cereale* evolved by introgression of self-incompatibility from *S. strictum* (Jaaska 1975). It was also assumed that non-brittle rye *S. cereale* subsp. *segetale* might be domesticated *in statu nascendi,* directly from some such hybrid populations currently extinct, while fragile subsp. *vavilovii* s.str. has persisted in the wild. Later, *S. sylvestre* was found to differ

from the other rye species also in allozymes of cathodal peroxidases CPX-4 and CPX-5 (Vences *et al.* 1987a) and chloroplast DNA (Muray *et al.* 1989; Petersen and Doebly 1993), whereas *S. cereale* and *S. strictum* revealed homologous polymorphism and could not be definitely distinguished by allozymes and chloroplast DNA (Vences *et al.* 1987b; Petersen and Doebly 1993). These data provide further support to my conclusion that *S. sylvestre* has not been involved in the origin of *S. cereale.*

Zhukovsky (1971) pointed out that there have been no reports of spontaneous appearance of non-brittle forms for more than 100 years of cultivation of wild and weedy ryes in different botanical gardens and collections. The reason may be in the recessive nature of the non-brittle mutation combined with the outcrossing breeding system of rye (Sybenga and Prakken 1962). The rare non-brittle mutants will remain phenotypically unexpressed in outcrossing rye populations in heterozygous genotypes until two parents with recessive non-brittle alleles cross and segregate into homozygotes in a progeny. The probability for this depends on the frequency of non-brittle mutations which may be extremely low. Therefore, the involvement of an inbreeding intermediate would be an important premise for the appearance of recessive non-brittle mutants phenotypically expressed in homozygotes.

Zhukovsky (1971) also has proposed a hypothesis that weedy subsp. *segetale* might have arisen from interspecific hybridization between wild perennial and annual ryes with the appearance of non-brittle forms in the hybrid progeny. He assumed that interspecific hybridization might be the crucial mutagenic factor which has caused the appearance of semi- and non-brittle forms of rye. Stutz (1972) noted that "on the slopes of Mt. Ararat, *S. vavilovii* makes contact and hybridizes rather freely with *S. montanum.*" The seed obtained from crosses between *S. cereale* and *S. strictum* were found to germinate only when *S. cereale* was the mother parent (Riley 1955), indicating that the introgression is possible from the perennial rye. Sympatric populations of wild perennial and annual ryes in the Near East region should be examined for the fragility, chromosome rearrangements and molecular characters in order to have more information about the origin of wild, weedy and cultivated forms of *S. cereale.*

Table 1. Electrophoretic variants of aliphatic and aromatic alcohol dehydrogenase (ADH and AAD), aspartate aminotransferase (AAT), acid phosphatase (ACP), esterase (EST) and anodal peroxidase (APX) isoenzymes in rye species: major electrophoretic variants (allozymes) are numbered in the order of their decreasing mobilities and listed in the order of decreasing occurrence; rare allozymes are labelled by letter 'r'; unique allozymes are in italics.

Species	ADH-A	AAD-A	AAD-E	AAT-B	AAT-C	ACP-B	EST-A	EST-B	APX-C
S. strictum	2;1r	1	2;1;3r	1	2;1	4;4f;5;3	2f;2;3	3;1;2	1
S. cereale									
subsp. *cereale*	2	1	2;1	1	2;3	4;1;3;2	2	1	1
subsp. *segetale*	2	1	2,1	1	2;3	4;1;3;2	2	1	1
subsp. *ancestral*	2	1	2;1	1;2r	2;3	4;3;1;2	2;2f;3r	1;3;2	1
S. iranicum	2	1	1	1	2	4	2	1	1
S. sylvestre	2	2	*1f*	1	2	*4f*	2;0	1	2

Source: Adapted from Jaaska (1975, 1983) and Jaaska and Jaaska (1984).

Barley

The cultivated barley *Hordeum vulgare* L., incl. *H. distichon* L. and *H. hexastichon* L., and its closest wild relative *H. spontaneum* C. Koch are autogamous annuals which with the allogamous perennial *H. bulbosum* L. share basic genome I (Von Bothmer and Jacobsen 1985). They also share a number of allozymes (Jaaska and Jaaska 1986; Jaaska 1992). Their hybrids are completely interfertile and have normal chromosome pairing in meiosis (Takahashi 1955; Zohary 1960). Cultivated barley and its closest wild relative, *H. spontaneum,* are now commonly recognized as subspecies of *H. vulgare* s.l. (Bowden 1959; Von Bothmer and Jacobsen 1985). However, taking into account their autogamous breeding system, which itself provides a reproductive barrier between them, and the fact that the biological species concept is not strictly applicable to uniparentals, they could formally be accepted at a species level as separate phylogenetic lineages.

There is a general agreement among investigators that cultivated barley has originated from its closest wild relative *H. spontaneum* through the latter's domestication (Takahashi 1955; Harlan 1968; Zhukovsky 1971; Trofimovskaya 1972; Von Bothmer and Jacobsen 1985; Zohary and Hopf 1993). Different views, however, have been expressed with respect to the place, time and mechanisms of the origin of different forms of cultivated barley, particularly six-row forms (Vavilov 1926; Åberg 1940; Nevski 1941; Takahashi 1955; Zohary 1959, 1960; Staut 1961; Bakhteyev 1964, 1975; Trofimovskaya 1972).

Monophyletic origin of the cultivated barley as a two-row form by domestication of *H. spontaneum* and the secondary origin of the six-row barley from a cultivated two-row form is now generally accepted (Zohary and Hopf 1993), thanks to experimental evidence on the secondary origin of the Tibetan semi-brittle six-row barley by hybridization between the cultivated six-row barley and wild *H. spontaneum* (Zohary 1959, 1960; Tovia and Zohary 1962). Therefore, this aspect of barley evolution is not discussed here.

Instead, I would like to focus attention on the appearance of non-brittle mutants in pure, wild populations of *H. spontaneum* as a critical issue in the domestication of barley which needs to be documented. The semi-brittle forms in the present-day mixed populations of weedy and cultivated barley are evidently derived by introgression from the cultivated barley. Genetic studies of hybrid progeny between *H. vulgare* and *H. spontaneum* have shown that ear fragility is controlled by two closely linked genes (*Bt* and *Bt2*) with a recessive mutation at either loci giving rise to non-brittle ears (Takahashi 1955).

In the case of a simple *in statu nascendi* domestication of barley by selecting out non-brittle mutants, the cultivated barley has evidently been domesticated repeatedly from different genotypes of wild barley, i.e. it has a polytopic origin. This, however, does not explain a strikingly wider morphological variability among cultivated barley than in other cereals. Indeed, morphological variation within *H. spontaneum* is limited to only three (Nevski 1941) or four (Bakhteyev 1962) botanical varieties which differ in the apex shape and awn length of lateral spikelets. At the same time, the cultivated barley is remarkably more variable with over 100 botanical varieties described among primitive barley landraces (Mansfeld 1950). Although a remarkable morphometric variation was observed among a set of 77 accessions of wild barley under cultivation around Moscow (Russia) under unusual climatic conditions, it still remained relatively limited and no non-brittle cultivar-like forms were observed (Bakhteyev 1979). Characters of the wild parent dominate in hybrids with cultivated barley and segregation appears in later generations. No morphologically new types were found among the progeny of hybrid generations between various morphological types of *H. spontaneum.* Therefore, the question as to why cultivated barley is so morphologically variable still remains unanswered.

Comparative studies of isoenzyme variation among a set of morphologically different accessions of *Hordeum vulgare* s.str. and *H. spontaneum* showed that both-had the same allozymes of essentially monomorphic isoenzymes and displayed variation of 10 polymorphic esterase isozymes (Table 2). This shows that the isozyme loci which were monomorphic in wild barley have remained also in the cultivated barley, i.e. cultivation has not induced new variation at the isozyme loci in contrast to those controlling variable morphological characters. The same also has been demonstrated with respect to wild and cultivated wheats and rye (Jaaska 1987). The cultivated barley and its wild progenitor could not definitely be distinguished by any of the isoenzymes studied except by a frequency of allozymes of some isoesterases.

Hordeum bulbosum displays extensive intrapopulation polymorphism of several isozymes which were largely monomorphic in *H. vulgare* and *H. spontaneum.* The allozyme genepool of the two annuals was found to be a subset of most frequent allozymes of *H. bulbosum* (Table 2). This result is consistent with a view that *H. spontaneum* might have evolved from *H. bulbosum* by fixation of genes controlling self-compatibility and annual habit. Isoenzyme data also argue against a multiple, polytopic origin of *H. spontaneum,* as well as against later, repeated introgression from the bulbous barley. Moreover, crossing experiments between *H. vulgare* s.l. and *H. bulbosum* have shown that hybrids could be obtained only by the embryo rescue technique, had disturbed meiosis, were sterile and frequently haploid owing to spontaneous elimination of *bulbosum* chromosomes (Kasha and Sadasivaiah 1971; Lange 1971).

Table 2. Electrophoretic variants of aliphatic and aromatic alcohol dehydrogenase (ADH and AAD), aspartate aminotransferase (AAT) and esterase (EST) isoenzymes in cultivated barley (*vulgare*) and its wild relative species (*spontaneum, bulbosum*)*:* major electrophoretic variants (allozymes) are numbered in the order of their decreasing mobilities and listed in the order of decreasing occurrence; rare variants are labelled by letter 'r'.

Isozyme	*vulgare*	*spontaneum*	*bulbosum*	*vulgare*	*spontaneum*
ADH-A	1	1	1;2r		
ADH-B	1	1	1		
ADH-D	3	3	3;2;1		
AAD-A	1	3	3;4;2;1		
AAD-B	2;0	2;0	2;2s;1;0		
AAD-E	2	2	2;1;3		
AAT-A	1	1;2	1		
AAT-B	1	1	1;2;3;0		

AAT-C	2	2	2;3;1		
EST-A				1	1
EST-B				1	1
EST-D				3;2;4;0	2;3;4;1;0
EST-E				2	2;1r;3r
EST-F				1;2;0	2;1;3;4
EST-H				2;0	2;1;0;3
EST-I				2;0;1;3	2;0;3;1
EST-J				1;0	1;0
EST-K				3;0;2	0;1

Source: adapted from Jaaska (1992) and Jaaska and Jaaska (1986).

Hordeum spontaneum and *H. bulbosum* are reproductively isolated by strong sterility barriers. Observations that crossability and chromosome elimination varies depending on the genotype of parental species suggested that introgression from the bulbous barley in some genotype combinations may be possible (Craig and Fedak 1985; Thomas and Pickering 1985).

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Plant-Gathering Versus Plant Domestication: An Ethnobotanical Focus on Leafy Plants - F. Ertug

Introduction

In this paper some information about the gathering of leafy plants in Turkey is presented. An ethnoarchaeological study on a contemporary rural village located close to a prehistoric site in Central Anatolia was carried out. It was observed that the village women gathered a large number of wild leafy plants. The number of species of plants gathered was much higher than expected considering that a sufficiently diverse variety of cultivated plants was available in their own gardens as well as in local markets.

Gathering of wild plants by contemporary villagers in Central Anatolia raised several questions about the domestication of leafy plants and our knowledge of human diets in the past. Through ethnobotanical study, answers to simple questions were attempted, such as: why do people continue to gather leafy plants thousands of years after domestication? What was the role of these plants in past diets?

Material and methods

The study area, the Melendiz Plain, is located on the Central Anatolian Plateau, southeast of Ankara, in the province of Aksaray. The modern town of Aksaray is in the southwest corner of Cappadocia, an ancient name once given to most of Central Anatolia. The Melendiz Plain is at an altitude of about 1100-2000 m asl, and is bordered by a range of volcanic mountains including Melendiz Dag (2935 m) and Hasan Dag (3268 m). The fertile plain is watered by the Melendiz Su and is suitable for cereal crops. The average annual precipitation is 339 mm. Most of the Aksaray area belongs to the Irano-Turanian floristic region, and is predominantly treeless steppe vegetation (Zohary 1973; Kürschner *et al.* 1995). The research area is in B5 square of the Flora of Turkey grid-system Map 1 (Davis 1965-1985). A considerable amount of information on plant-gathering and a large

collection of plants were obtained during the fieldwork in the Melendiz Plain. The use of the plants for food, fuel and fodder, as well as in textiles, basket-making, drugs, glues, brooms, dyes, amulets and medicines was documented. Of the 600 plant specimens that were collected, 313 belong to 205 genera and 70 families. Most of the identifications were made by Professors Tuna Ekim, Mecit Vural and their team in the Department of Biology, Gazi University, Ankara, and the samples were deposited in the Gazi University Herbarium.

Another indigenous vegetation belt once surrounded this steppe vegetation (Davis *et al.* 1988). Zohary (1973) uses the term Xero-Euxinian vegetation belt for an area with lower average precipitation than the mediterranean zone, and with increasing continentality toward the Central Anatolian plateau. This belt of 'steppe-forests' starts east and south of the research area, where the altitude reaches 1400 m. The dominant tree in the deciduous forests is *Quercus cerris;* a mixed forest of *Q. pubescens, Q. infectoria, Q. ithaburensis,* in addition a few *Q. trojana,* occurs in the area, and *Q. vulcanica* is found at 2000 m, on the slopes of the Melendiz Mountains. Neither *Pinus* nor *Juniperus* is represented in the present steppe-forest, but the species that originally grew together with *Pinus nigra,* such as *Q. vulcanica* and *Acer hyrcanum* subsp. *tauricolum,* are still present. Solitary wild fruit trees of *Pyrus elaeagrifolia* and *Crataegus* species indicate the lower limits of the forest-steppe, at about 1200 m.

There are also some small patches among the volcanic areas, where *Crataegus, Celtis, Prunus, Pyrus* and *Amygdalus* trees have survived, and marshy areas nearby that contain many species used for mat- and basket-making, such as *Typha* and *Phragmites.* The rivers and small streams that provide moisture for the grazing lands are bordered by some edible species such as *Berula erecta, Rorippa nasturtium-aquaticum* and *Veronica anagallis-aquatica. Triticum boeoticum* (einkorn) and some wild species of *Hordeum* are also present in patches. Today, most of the area is devoted to cereal production with gardens near available water, and partly to orchards and vineyards, so the area is predominantly a man-made (anthropogenic) landscape.

The village of Kizilkaya, central to this study, is about 25 km southeast of the city of Aksaray, and 1 km north of an archaeological site Asikli Höyük. This Pre-Pottery Neolithic site, which dates from 8000 to 7450 years BP (calibrated), has been under excavation for the last eight years by a team from the University of Istanbul (Esin *et al.* 1991; Esin 1996). The excavations indicated that the economy of Asikli was based on crop husbandry (van Zeist and de Roller 1995), on hunting game animals and gathering wild plants. The ethnoarchaeological fieldwork was conducted from January 1994 to the end of June 1995 to provide comparative data to aid in the interpretation of the archaeological remains from Asikli. Plant-gathering was an important aspect of the economy of an early Neolithic settlement, but has not been previously studied in Anatolia.

Specimens of all plants gathered by the village folk were collected, pressed and put in a card file according to the local names of the plants. Questionnaires, one for the men concerning land-ownership and agriculture, and one for the women about plant-gathering and gardening, were completed. Thirty households were chosen randomly from three income groups, so that different attitudes of rich and poor toward gathering and/or agricultural decisions could be detected. These questionnaires helped to quantify the number of wild plants that each woman knew and gathered. However, the most satisfactory way to collect information about the plants was to accompany and question the women while they were gathering, as well as to attend all agricultural activities, such as planting, weeding, harvesting, preparing and cooking.

Results

The modern village of Kizilkaya has a population of about 1300 occupying 300 houses, and its economy is based on agriculture, field-cropping and gardening, as well as the husbandry of sheep and cattle. The total number of known cultivars is 70, and of these 20 are trees, 10 are used primarily as animal fodder, 4 species are no longer cultivated, and some others are planted only rarely. The basic cereal crop is bread wheat, and basic legumes such as beans, lentil and chickpea are also grown. About 20 vegetables are more or less regularly planted in spring and consumed during summer, and some are dried, made into paste or pickled, and stored for winter.

Onion, potato, garlic, green beans, squash, pepper and tomato are the most important. Beet, spinach, cabbage, leek, purslane, green onion, cress, lettuce, parsley and chicory are regularly planted for the consumption of their green leaves. Whereas the number of green leafy vegetables does not exceed 10 during the summer, as many as 40 different kinds of wild greens are gathered during the winter and spring. Gardening is a recent development within the last 20 to 30 years, and as the climate is continental, and the frosts start as early as October, it is strictly limited to the summer.

Until recently, fresh products of the village gardens, such as tomato and leek, could be eaten up to October, but from November to June, a period of 7 to 8 months, no fresh vegetables would be available. This was true until about 20 to 30 years ago, but since transportation became available, fresh vegetables and fruits can be found in the local village markets all year round. Despite this easy accessibility, the local tradition of gathering wild plants for food persists in Central Anatolia, and probably goes back at least 500 years. Historical records for many

villages in this area go back to the early 16th century (Ertug-Yaras 1997).

Over 100 wild species of plants in and around the Melendiz Plain are considered by the local people *as* edible (Ertug-Yaras 1996). These edible species belong to 36 botanical families. Among these, 42 wild greens make up the most commonly and regularly consumed group (see Appendix), other than wild fruits, roots and stems. Among the 42 greens in 18 families, species belonging to the Asteraceae and Brassicaceae families are the most numerous. Twelve of these greens (see (*) in the Appendix) were not previously recorded in the literature as edible.

Wild greens are an important component of the local diet, and are regularly gathered from October to June. During the winter, unless there is deep snow, it is possible to find green leaves of 13 to 16 different varieties of edible plants. Three different kinds of edible aquatic plants can be found, even when the ground is covered with snow, but these are frozen if the temperature drops below zero, or are destroyed when there is spring flooding. The maximum number of plants with edible leaves is gathered in April and May, 33 and 35 respectively, while in June there are only 9.

The gathering of leafy plants is exclusively carried out by women. Groups of women, mostly with their children, go to gather greens during winter and spring, when fresh greens are most needed in the diet. Most of these greens are eaten raw with salt between folds of the local flat bread (yufka), but some greens require cooking. These are chopped and cooked together with onions and cracked wheat. These dishes are called 'cacik', and are usually eaten with yogurt.

According to the questionnaires, women in middle-income and poorer groups go more often, and gather more greens than do women in more affluent households. Low-income women also gather more species than do the richer households, but they are less selective. The implication is that gathering wild greens is related to nutrition and taste more than to economic need.

Nutritional analysis for twelve of the most commonly consumed wild plants indicates that these plants are a very good source of raw protein and minerals (Ertug-Yaras 1997). Most of them have protein and mineral values as high as cultivated green vegetables, and probably make a significant nutritional addition to local diets.

Some women in the village of Kizilkaya told me that they made several attempts to cultivate the wild plants in their gardens, but have found that the desirable sharp or bitter taste of the wild plants changes when they are planted in gardens. This is probably an important reason why so few of the many leafy plants were selected for cultivation. Chicory, *Crepis foetida* and wild spinach were the most common experiments. These showed phenotypic changes, with larger leaves, as well as different tastes. Some villagers attribute these changes to water availability, some to the soil, and some botanists explain it as a reaction of the plants to reduced competition for water and nutrients. Wild spinach (*Spinacia tetranda*) and wild beet (*Beta macrorrhiza*) grow in fallow fields and waste places and find their place in the diet while their domesticated relatives grown from commercial seeds bought in the market are commonly planted in gardens.

Discussion

Some of the reasons village women of all economic groups still gather leafy plants became apparent during the fieldwork: (1) the villagers feel the need for green leafy plants in their diet all year round, and in winter and spring when these are not available from their own gardens the women gather the wild plants; (2) these plants grow abundantly in most areas during winter and spring, are easy to gather, and most require no processing except washing; (3) their taste seems to play an important role in their dietary use, perhaps because they add variety to the otherwise monotonous diet; (4) gathering is also a social activity, as the women take pride in providing for their families, and also share the plants they gather with their friends and neighbors. The women consider plant-gathering a pleasant way to get out of the house and to socialize with other women; (5) gathered greens, as well as bulbs, roots, mushrooms and fruits, provide a buffering/risk-management technique against potential hunger.

The drive to gather wild plants is closely related also to insecurity during the times of scarcity, such as droughts, epidemics, wars or rebellions. Recent reports about strife in North Korea, Bosnia and various parts of Africa have indicated that wild food may make the difference between survival and death when crops fail repeatedly, or when harvests are stolen or destroyed. While this critical economic aspect of plant-gathering is frequently emphasized, we tend to forget or consider unimportant the role of wild plants in the daily diet.

Archaeobotanists considering past diets usually emphasize recovery and study of cereals and pulses, especially their initial domestication and early use. Although the primary role of cereals in the subsistence of both modern and past societies is extremely important, the role of vegetables, mushrooms and soft fruits tends to be ignored, and, of course leaves, stems, flowers and bulbs are very difficult to find among archaeobotanical remains. Only very recently have techniques been developed for the recovery of such plant parts. In general, as soon as the

domestication of cereal crops is detected on a site, it should not be assumed that people limited themselves to these cultivated cereals, and stopped using wild plants as food.

Ethnobotanical studies in various countries indicate that while farmers restricted themselves to a limited number of crops, their wild plant kit, used as food and for other purposes, is much larger. Farmers use this knowledge and pass it on to future generations, and they do not limit themselves to the surrounding environment, but trade with other villages for plants not available to them.

Conclusions

Wild plant-gathering in Central Anatolia is not unique to this region, nor to Anatolia itself. It is true that the development of agriculture and the grazing of animals have decreased the availability of wild plant sources, but unless there is very dense population, many resources are still available. A good indication of this is that even after thousands of years of agriculture and animal grazing in the Melendiz area, more than 100 edible species, mostly perennials, are still available and consumed. Although not well studied, wild plant-gathering is a common tradition among farming societies in the Near East. The role played by women in early agriculture and plant-gathering and domestication should not be underestimated.

It is hoped that the role of wild leafy plants in the diet of agricultural societies and local traditions of wild plant use can be better understood through further ethnological studies, and that they will illuminate archaeological research to provide better understanding of past diets. Perhaps such studies can help improve diets to suit future environmental changes.

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Appendix: Edible greens of the Melendiz area, Aksaray, Turkey (B5).

Family	Species[†]	Local names	Gathering frequency[‡]
Amaranthaceae	*Amaranthus retroflexus* L.	Pancar otu	XX
Apiaceae	*Berula erecta* (Huds.) Coville (*)	Kazayagi	XXX
Asteraceae	*Centaurea depressa* Bieb. (*)	Gökçebas	X
Asteraceae	*Chondrilla juncea* L. var. *Juncea*	Karaavlik	XXX
Asteraceae	*Cichorium intybus* L.	Çitlik/Yabani hindiba	XXX
Asteraceae	*Crepis foetida* L. subsp. *rhoadifolia* (Bieb.) Celak. (*)	Kohum otu	XXX
Asteraceae	*Lactuca serriola* L.	Marul otu/Yazi marulu	XXX
Asteraceae	*Scariola viminea* (L.) F.W. Schmidt	Kedi çitligi	X
Asteraceae	*Scorzonera cana* (C.A. Meyer) Hoffm. var. *radicosa* (Boiss.)	Tekercik/Dede sakali	XXX
Asteraceae	*Sonchus asper* (L.) Hill subsp. *glaucescens* (Jordan) Ball	Su kangali	X
Asteraceae	*Taraxacum microcephaloides* van Soest (*)	Ebem çitligi/Karahindiba	XX
Asteraceae	*Taraxacum serotinum* (Waldst. et Kit.) Poiret (*)	Çukur çitligi	X
Asteraceae	*Tragopogon buphthalmoides* (DC.) Boiss.	Yemlik	XXX
Boraginaceae	*Anchusa undulata* L. subsp. *hybrida* (Ten.) Coutinho (*)	Ballik	X
Brassicaceae	*Barbarea plantaginea* DC. (*)	Götlez götü	XXX
Brassicaceae	*Camelina hispida* Boiss. (*)	Bozot	XX
Brassicaceae	*Capsella bursa-pastoris* (L.) Medik.	Kuskus ekmegi	XXX
Brassicaceae	*Rorippa nasturtium-aquaticum* (L.) Hayek (Syn. *Nasturtium officinale* R.Br.)	Aci tere	XXX
Brassicaceae	*Sinapis arvensis* L.	Hardal otu	XXX
Brassicaceae	*Sisymbrium altissimum* L. (*)	Elgelen hardali	X
Campanulaceae	*Campanula cymbalaria* Sm. (*)	Yer otu	X
Caryophyllaceae	*Silene vulgaris* (Moench.) Garcke var. *vulgaris*	Tavsan ekmegi	XX
Caryophyllaceae	*Stellaria media* (L.) Vill. subsp. *pallida* (Dumort.) Aschers. et. Graebn.	Haval otu	X
Chenopodiaceae	*Beta macrorrhiza* Stev.	Kizil pancar	XX
Chenopodiaceae	*Chenopodium album* L. subsp. *album*	Köpürgen otu	X
Chenopodiaceae	*Chenopodium album* L. subsp. Aellen *iranicum*	Sirken otu	X
Chenopodiaceae	*Spinacia tetrandra* Stev.	Yazi ispanagi	XX
Convolvulaceae	*Convolvulus lineatus* L (*).	Tavsan kulagi	XX
Crassulaceae	*Sempervivum armenum* Boiss. et Huet var. *armenum*	Musluk otu	X
Fabaceae	*Ononis spinosa* L. subsp. *leiosperma* (Boiss.) Sirj.	Sigek dikeni	X
Geraniaceae	*Erodium cicutarium* (L.) L'Hérit. subsp. *cicutarium*	Innelik	XXX
Malvaceae	*Malva neglecta* Wallr.	Ebemgümeci	X
Malvaceae	*Malva sylvestris* L.	Ebemgümeci	X
Papaveraceae	*Papaver rhoeas* L.	Gül otu/Gelincik	XX
Polygonaceae	*Polygonum bellardii* All. (*)	At mercimelegi	X
Polygonaceae	*Polygonum cognatum* Meissn.	Mercimelek	XX
Polygonaceae	*Rumex acetosella* L.	Eskileme/Kuzum oglagi	X
Polygonaceae	*Rumex crispus* L.	Kazan kulpu	X
Polygonaceae	*Rumex scutatus* L.	Eskileme	XX
Portulacaceae	*Portulaca oleracea* L. subsp. *oleracea*	Temizlik otu/Semizotu	XXX
Scrophulariaceae	*Veronica anagallis-aquatica* L	Camak	XXX

Urticaceae	*Urtica dioica* L.		Cizlagan/Isirgan	X

† (*) mark at the end of species' names indicates that these are not reported as edible in the literature.

‡ The 'Gathering frequency' column offers an impressionistic and tentative evaluation: x-rarely gathered; xx - commonly; xxx - most commonly gathered species.

Origins and Domestication of Mediterranean Olive Determined through RAPD Marker Analyses - G. Besnard, A. Moukhli, H. Sommerlatte, H. Hosseinpour, M. Tersac, P. Villemur, F. Dosba and A. Bervillé

Introduction

Olive (*Olea europaea* L.) is one of the most important cultivated trees in the Mediterranean basin and the spread of its cultivation was associated with that of grapevine, almond and fig. These species form the oldest group of domesticated trees (Zohary and Hopf 1993).

Olea europaea is a complex of four subspecies (Table 1, Fig. 1) (Green and Wickens 1989). *Olea europaea* subsp. *europaea* is separated into two taxa: var. *sylvestris* (oleasters: feral and wild forms) and var. *sativa* (cultivated forms). Cultivated trees could develop from oleasters (Zohary and Spiegel-Roy 1975).

The area of olive domestication appears to have been the Near East. Artifacts associated with the oil-extraction process as well as those associated with clonal propagation are the main evidence for domestication which occurred during the early Bronze Age (Liphschitz *et al.* 1991). Nevertheless, the exploitation of wild forms before domestication is suggested by discoveries of olive tree remains in archaeological sites since Palaeolithic times about 43,000 years BP (Zohary and Spiegel-Roy 1975). This was not specific to the Near East. On the basis of archaeobotanical evidence, Terral and Arnold-Simmard (1996) and Galili *et al.* (1989) have suggested a pre-domestication period in eastern Spain and Palestine. During this period, harvesting and caring of wild trees could have occurred without vegetative multiplication, thus leading to higher production. Evidence of olive remains from the Holocene, outside the natural distribution of the species, has been observed at a Syrian archaeological site (Willcox 1996) but the low frequency of olive fragments is insufficient to conclude that domestication occurred there.

The number of generations required for the improvement and selection of cultivated forms is likely to be very low in comparison with annual plants. A close genetic similarity is therefore expected between wild forms and their direct cultivated descendants (Liphschitz *et al.* 1991). Elant (1976) has suggested that cultivated forms were propagated in the entire Mediterranean basin and crosses between them and with local wild forms have led to the creation of new cultivars. At least, the crosses between related species of the *Olea europaea* complex could have occurred in different areas (northern Africa, the Middle East and the Canary Islands). In southern Morocco, *O. maroccana* has been considered as an intermediate form between *O. europaea* and *O. laperrinei* by Sauvage and Vindt (1952) or as a variant of *O. laperrinei* (Maire 1933; Green and Wickens 1989; Zohary 1994). The distribution area of this form could overlap with the cultivated form (Zohary 1994). Some examples of spontaneous interspecific crosses are known for several cultivated trees, notably apple, pear, date palm and grapevine (Zohary and Hopf 1993). Consequently, the origin of Mediterranean olive is not clear. Two places have been suggested: North Africa (Maley 1980) and the Near East (Chevalier 1948; Turrill 1951).

Table 1. The *Olea europaea* L. complex: subspecies and their main taxa.

Subspecies		Geographical origin
subsp. *europaea* Mansfield		
	- *O. europaea* L.	
	var. *sylvestris* D.C. (oleasters)	Mediterranean basin
	var. *sativa* Lehr. (cultivars)	Mediterranean basin
subsp. *laperrinei* Ciferri		
	- *O. laperrinei* Batt. & Trab.	Saharan Mountains
	- *O. maroccana* Gren. & Burd.	Atlas Mountains (Morocco)
subsp. *cerasiformis* Kunk. & Sund.		Canary and Madeira Islands
subsp. *cuspidata* Ciferri		

- *O. cuspidata* Wall.	Asia	
- *O. chrysophylla* Lam.	Arabia, Abyssinia	
- *O. africana* Mill.	Eastern and southern Africa	

A molecular analysis of different wild and cultivated accessions could clarify the origins of the domestication and of the selection of olive trees. The RAPD markers have been used to identify cultivars (Koller *et al.* 1993), to reveal the extent of diversity (Isabel *et al.* 1995) and to differentiate species for detection of interspecific hybridization (Jeandroz *et al.* 1996; Vigouroux *et al.* 1997) or in a phylogenetic approach (Wang *et al.* 1994). In this preliminary study we chose cultivars and wild forms with RAPDs to estimate the similarities between them.

Material and methods

Plant materials

Sixty-four cultivars from different countries around the Mediterranean basin were analyzed (Table 2). These cultivars were selected from a germplasm collection maintained at Montpellier (France) and provided by Dr Rallo (Cordoba) and Dr Baldoni (Perugia) from the collections of Cordoba (Spain) and Perugia (Italy).

Oleasters (wild olive trees) were studied from three sources: from Corsica (11 individuals: 'Corsica 1' to '11'), from Morocco (9 individuals: 'Morocco 1' to '9'), and from southern France (5 individuals: 'Hérault 1' to '5'). We have no criteria to distinguish wild from feral forms. Four individuals of *O. maroccana* from southern Morocco and four individuals of *O. europaea* subsp. *cuspidata* from four different areas [Kenya (*O. africana*), Iran, India, China] were also studied.

Molecular analysis

DNA preparation was carried out according to a modified method described by Saghai-Maroof *et al.* (1984). Five grams of leaves were ground and 20 ml of 2X CTAB buffer (100 mM Tris-HCl pH 8,1.4M NaCl, 20 mM EDTA, CTAB 2%) were added with 0.2 ml of βmercaptoethanol. This mixture was incubated at 65°C for 1 hour. Ten milliliters of chloroform/isoamylic alcohol (IAA) (24/1) were added and mixed at 100 rpm for 20 min. This mixture was centrifuged at 4500 rpm for 20 min. The supernatant was recovered and 10 ml of chloroform/IAA(24/l) were added and mixed at 100 rpm for 20 min. This mixture was centrifuged at 4500 rpm for 20 min. The supernatant was recovered and mixed with 20 ml of isopropanol and stored at -20°C overnight. The DNA pelot was recovered, washed with ethanol solution (ethanol 76%, 10 mM ammonium acetate), dried, and removed in 0.5 ml of 1X TE (10 mM Tris-HCl pH 8,1 mM EDTA). Then 500 µg of RNAse A (Boehringer) were added. The incubation was performed at 37°C for 1 hour; 530 µl of phenol/chloroform/IAA (25/24/1) were added and mixed. After centrifugation at 12,000 rpm for 10 min, the supernatant was recovered and mixed with 530 µl of chloroform/IAA (24/1). Another centrifugation was performed at 12,000 rpm for 10 min, and then the supernatant was mixed with 1 ml of ethanol and 188 µl of 7.5M ammonium acetate solution. This mixture was kept overnight at -20°C. A final centrifugation at 14,000 rpm for 10 min was performed to recover DNA pelot which was dried, then dissolved in 0.5 ml of 1XTE.

Fig. 1. Herbarium samples of *Olea europaea* taxa. A = *O. africana* (Reunion Island); B = *O. chrysophylla* (Yemen); C = *O. laperrinei* (Algeria); D = *O. europaea* var. *oleaster* (feral?-France); and E = *O. europaea* var. *oleaster* (Corsica).

Table 2. List of *Olea* cultivars studied according to their geographic origins.

Geographical origin	No. of cvs.	Cultivars
Maghreb	9	Barouni, Bid el Hamam, Chemlal de Kabylie, Chemlali de Sfax, Chetoui, Meski, Picholine Marocaine, Sigoise, Zarazzi
Iberian Peninsula	8	Arbequina, Cornicabra, Empeltre, Galega, Lechin de Sevilla, Manzanilla, Picual, Villalonga
France	20	Amellau, Belgentier, Bouteillan, Cayet Bleu, Cayet Rouge, Cayon, Colombale, Corniale, Filitosa[†], Sabina, Lucques, Olivière, Picholine, Picholine de Rochefort, Pigale, Rougette de Pignan, Tanche, Verdale, Verdelet, Vermillau
Italy	11	Ascolana Tenera, Cassanese, Cellina, Dolce Aggogia, Frantoio, Giarraffa, Leccino, Leucocarpa, Nocelara del Belice, Pendolino, San Felice
Yugoslavia	1	Oblitza

Greece	6	Amygdalolia, Carolia, Gaïdourolia, Kalamata, Koroneiki, Valanolia
Turkey	4	Ayvalik, Domat, Sofralik, Uslu
Near East	4	Kaissy, Merhavia, Souri, Zaity
Egypt	1	Toffahi
Total	64	

[†] 'Filitosa' corresponds to a cultivar which was identified by the authors at the Filitosa archaeological site in Corsica (France) without known denomination.

The procedure for obtaining RAPD markers has been described by Quillet *et al.* (1995). Thirty decamer primers (Bioprobe) were tested on eight genotypes: five cultivars ('Olivière', 'Lucques', 'Giarraffa', 'Arbequina', 'Domat'), two wild forms corresponding to the *cuspidata* subspecies (from Iran and China) and *Ligustrum vulgaris* L. as an outgroup. The choice of primers was based on the level of polymorphism with the clearness of banding profiles.

Data exploitation

The bands were noted and coded according to the primer and the size of the fragments as judged with the 1 Kb ladder from BRL as reference. Several individuals from 15 cultivars were analyzed; fragments, which were not reproducible, were not taken into account here. The probability to obtain the same pattern for two different cultivars was calculated according to the formula from Nybom and Hall (1991): (mean of Nei and Li similarities)/Mean of marker number by individual.

A Factorial Correspondence Analysis (FCA) was performed on the data with the procedure CORRESP from SAS (SAS 1992) to show the structure of the data. Distances between all individuals were computed according to Sokal and Michener's index (Sokal and Michener 1958): $d_{ij} = a + d/a + b + c + d$, where a is the common band between two individuals, i and j, b and c the bands present in one individual (i or j, respectively), and d the common absence of bands between the two individuals i and j. Dendrograms were constructed with the UPGMA algorithm (Benzécri 1973).

Results

Out of 30 primers checked, 6 (A1, A2, A9, A10, C15, E15) were retained because they reveal the highest level of polymorphism. These were then applied on all the individuals. They enabled us to note 101 markers. Thirteen are conserved in *Olea* individuals and three are conserved between *Ligustrum vulgaris* and *Olea* genus on the basis of size homology. Twenty-three markers are unique to *L. vulgaris.*

Specific markers were found only for related species: four for O. *maroccana* and one for O. *cuspidata* from Asia. We have one unique marker for 'Lechin de Sevilla' (Spain) and another for 'Zaity' (Near East). The cultivar markers have a mean frequency of presence (0.57) lower than that in wild populations (superior to 0.69)(Table 3).

Analysis and comparison with oleaster cultivars

Most cultivars (56/64) are differentiated with our markers. Four couples of cultivars cannot be distinguished: 'Picholine Marocaine' and 'Sigoise', 'Cellina' and 'Frantoio', 'Meski' and 'Bid el Hamam', 'Belgentier' and 'Merhavia'. The probability to obtain the same pattern for two different individuals was $3.9 \cdot 10^{-4}$ (for Mean of Nei and Li similarities = 0.592 and Mean of marker number by individual = 14.98).

The first dimension (13.9%) of the FCA performed on the cultivar data permitted separation of 'Chemlal de Kabylie' from the other cultivars. On the other dimensions (explaining less than 9% of the variability) several cultivars are separated, namely 'Zaity' and 'Lechin de Sevilla' (data not shown). FCA of Mediterranean olive trees (wild, feral and cultivars) separated wild forms from both Corsica and Morocco, 'Sabina', 'Filitosa', 'Chemlal de Kabylie', 'Galega' and 'Koroneiki' from the rest of the individuals. We found 13 markers present in oleasters from the Western Mediterranean and absent in all cultivars from the Near East (except 'Koroneiki' from Crete). Seven of these markers are present in the five cultivars clustered with the oleasters from Morocco and Corsica.

Analysis of the wild forms

The FCA constructed with wild form data only enabled us to distinguish four groups corresponding to: (1) *O. europaea* from Mediterranean basin, (2) *O. maroccana* from southern Morocco, (3) *O. africana* from Kenya, and (4) *O. cuspidata* from Asia.

Phenogram constructed with total data

On the phenetic tree constructed on the total data (Fig. 2), a clear structure fitting a geographic origin of Mediterranean olive was not obtained but small groups corresponding to regions were found. The oleasters are related with cultivars. The oleasters from Corsica and from Morocco form homogeneous groups (except for 'Morocco 5' and '6' which are related with 'Picholine Marocaine') in contrast to wild forms from southern France. The oleasters from Corsica and from Morocco form a subgroup (subgroup 1.2) and are related with 'Chemlal de Kabylie' (Algeria), 'Filitosa' (Corsica), 'Sabina' (Corsica), 'Galega' (Portugal), 'Pigale' (France) and 'Koroneiki' (Crete). The forms from Asia (*O. cuspidata*) and from Africa (*O. maroccana* and *O. africana*) form two well-separated groups.

Fig. 2. Dendrogram based on Sokal and Michener (1958) distances computed between all studied individuals and constructed according to UPGMA algorithm. The index numbers correspond to the geographic origin of the individuals: 1 = eastern Mediterranean basin; 2 = Italy and Yugoslavia; 3 = France; 4 = Iberian Peninsula; 5 = Maghreb; and 6 = Asia.

Discussion

Analysis of cultivars in relation to oleasters

RAPDs permit identification of most cultivars. The probability of obtaining the same pattern between two different cultivars is very low ($3.9x1^{-5}$). Nevertheless, we cannot eliminate the possibility that occasional mutations can generate phenotypic variations leading to different clones. Such a phenomenon has been reported in numerous vegetatively propagated species (Zohary and Hopf 1993).

The pattern obtained does not show a clear geographic origin of the olive. This can be expected because of commercial exchanges between the different countries of the Mediterranean basin since antiquity. It seems that there exists a high variability in cultivated olive. The number of polymorphic markers is higher in the cultivar group than in the wild populations but this depends on the population size which is insufficient here to detect all polymorphic markers (Table 3). Crosses between forms of different geographic origin have occurred and this probably explains the large genetic diversity (Elant 1976). Thus, a high level of heterozygosity is therefore expected and the low mean frequency of present markers in the cultivar group reflects this fact.

Some varieties which differentiate from the rest of cultivars support the theory that selection of olive occurred in different places. Since 'Chemlal de Kabylie' is male-sterile (Ouksili 1988), we suggest this cultivar is derived from an interspecific hybrid.

In contrast to oleasters from Corsica and Morocco, the trees from southern France are very close to cultivars. These forms did not exhibit specific or unique markers and this suggests that they are feral forms. The present climate of southern France is not favorable for the continued existence of indigenous forms (Zohary and Hopf 1993) although these existed during the Holocene in this region (Solari and Vernet 1992). The occurrence of relics of former populations is, therefore, likely.

Relationships between species of *O. europaea* complex

Olea maroccana is closely related to *O. africana* from Kenya. This supports the Maley hypothesis (1980) of a tropical origin of *Olea* (*O. laperrinei*) in the mountains of North Africa. The distribution of *O. laperrinei* in the Atlas Mountains is unknown (except for *O. maroccana*). *Olea maroccana* is certainly a relic of an ancient population of tropical *Olea.* Other relic populations could exist locally and we suggest that *O. laperrinei* was distributed all over the mountains of Maghreb. The sympatry between cultivated forms and *O. maroccana* is suggested by Zohary (1994) and we can predict that they may hybridize. The existence of introgression of *O. maroccana* in cultivated forms is therefore possible but not detected yet. On the basis of our molecular data, *O. africana* appears intermediate between *O. cuspidata* and *O. maroccana.* It is differentiated from *O. cuspidata* from Asia, suggesting a differentiation between Asian and Eastern African forms as suggested by Zohary (1994) because of the discontinuous geographical distribution and an adaptation to different environments. We recognized the different subspecies as described by Green and Wickens (1989) and we will be able to detect easily any hybrids.

The origin of olive by hybridization between oleasters and related species suggested by Elant (1976) is not supported here. We now have to verify whether *O. chrysophylla* is related to the cultivated forms from the Mediterranean basin as suggested by Chevalier (1948).

Table 3. Mean frequency of present markers and percentage of polymorphic markers in studied populations and cultivar group.

Groups of individuals	No. of individuals	No. of polymorphic markers	Mean freq. of present markers	$R_{p/c}$[†]
Corsica 1 to 11	11	25	0.69	0.61
Morocco 1 to 9	9	22	0.76	0.55
Hérault 1 to 5	5	26	0.71	-
O. maroccana	4	19	0.82	-
Cultivated forms	64	37	0.57	0.71

[†] $R_{p/c}$ corresponds to the following ratio - number of polymorphic markers: number of conserved markers in the group of individuals. The number of individuals studied in *O. maroccana* and southern France populations is insufficient to consider this ratio.

Conclusion

The present-day olive cultivars may have derived from oleasters of different Mediterranean areas. Human migration and exchange of germplasm have increased variability of the cultivated and the wild forms. Nevertheless, the classification of the indigenous wild forms in the Mediterranean basin is awaited. Evidence of hybridization with related species was not found, although two origins of *Olea* in the Mediterranean basin are suggested (Middle East and North Africa). The present study is preliminary and analysis of several more accessions of cultivated and wild forms is needed, particularly of the related species (*O. chrysophylla* from Yemen, *O. laperrinei* from Hoggar) to verify our results.

Acknowledgment

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Part 3. Archaeobotanical Evidence for Agricultural Transitions

Identifying Pre-domestication Cultivation Using Multivariate Analysis - S. Colledge

Introduction

An analytical method for assessing the composition of archaeobotanical assemblages is presented in this paper. The method highlights the differences between suites of plant taxa found on certain early sites in the Levant and the establishment of 'vegetational fingerprints' is proposed. Explanations for the differences in the taxonomic compositions of the assemblages are given in terms of the differences in the vegetation at the sites and, in particular, in the changing 'management' of the landscape by cultivation.

The work is based on a large body of published data from several sites in Syria (van Zeist and Bakker-Heeres 1982, 1984, 1986), and it stems from an investigation of plant exploitation on early prehistoric sites in the Levant (Colledge 1994).

Modern experimental work has confirmed that certain methods of land preparation and harvesting are prerequisites for an increase in numbers of wild cereals with the 'domestic-type' genetic mutation (i.e. in the gene controlling the toughness of the cereal rachis), such that if these techniques were practised over a considerable period of time they would lead to the dominance of fully domestic crops (Hillman and Davies 1992). In antiquity, therefore, pre-domestication cultivation (i.e. the cultivation of wild cereals) would have been a necessary stage in the evolution of domestic cereal species. It has also been proposed that a progressive increase in human energy input into the land would have been necessary to maintain productivity at and after the inception of cultivation (Harris 1996).

Changes in the material culture (including differences in types and abundance of groundstone and flint artefacts) in the Natufian period have been attributed to a greater use of plant resources.

> "Even though the primary source of subsistence in the Natufian seems to have been animal resources, it was possibly the consistent utilization of plant resources that produced the ecodemographic and material cultural changes from the Palestinian Upper Palaeolithic tradition." (Henry 1973:189-190)

The Natufian period is the cultural entity immediately preceding the period during which the first domesticated cereals have been found in the Levant (the period known as the Pre-Pottery Neolithic A, or PPNA). It is thought that during this time the first efforts at plant management, or cultivation, took place. There has been a long history of speculation about the possibility of pre-domestication cultivation of wild cereals during the Natufian period, and speculation has been accompanied by attempts to look for evidence (whether direct or indirect) of it having taken place at sites in the Levant. Two examples of potential sources of evidence in the archaeological and archaeobotanical records are described here.

Experimental use of modern flint sickle blades to harvest wild cereals seemed to demonstrate that the microwear (i.e. alteration to the surface of the flint in the form of polish or grooves) produced on the tools was distinctive if the soil the plants had grown on was cultivated (i.e. tilled) (Unger-Hamilton 1989:101). After comparison with the microwear on ancient blades, Unger-Hamilton concluded that wild cereals were being cultivated in the Early Natufian. Recent studies have shown, however, that there is not necessarily a direct correlation between surface alteration of flint and specific worked materials (Levi Sala 1996:68-69), and so the conclusion that Natufian sickles had been used to harvest cultivated wild cereals must be questionable.

It was suggested that there may have been histological changes to the cells in the outer layers of the grains of wild cereals which had been exposed to cultivation (Hillman *et al.* 1989:242-243), prior to the evolution of the domestic species (with the obvious domestic characteristics). Micromorphological investigations proved that no such changes were manifest in modern populations of wild cereals that were found growing alongside domestic crops (Colledge 1988; Hillman *et al.* 1989).

Despite these attempts and others, however, no clear, undisputed evidence has been found in the archaeological and archaeobotanical records that would favor pre-domestication cultivation having taken place.

Identification of 'vegetational fingerprints' in the archaeobotanical record

The published data from five Syrian tell sites have been used in this study. The sites are Tell Mureybit, Tell Aswad, Tell Ghoraifé, Tell Ramad and Tell Ras Shamra. Figure 1 shows the geographic location of each of the sites and Figure 2 gives the ^{14}C dates. Tell Mureybit is situated on the northern bank of the Euphrates River, in the 'elbow' of the river course before it flows eastward to join the Belikh River (van Zeist and Bakker-Heeres 1986:171-173). The site lies within the Irano-Turanian phytogeographical region, in an area of heavily denuded steppe and desert vegetation. At the time the site was occupied the Euphrates Valley would have been covered with poplar forest. Tell Aswad, Tell Ghoraifé and Tell Ramad are all situated in the Damascus Basin, in southwestern Syria (van Zeist and Bakker-Heeres 1982:168-173). The basin is bordered on the west by the eastern escarpments of the Anti-Lebanon Mountains, to the north by the limestone hills of the Palmyra range, and to the south and east by the basalt outcrops of the Hauran Plain. Tell Aswad and Tell Ghoraifé are both located in the eastern part of the basin, within an area bounded by the shores of an ancient Pleistocene lake. They are in the vicinity of two extant lakes, Lake Aateibé and Lake Hijjâné, fed by perennial streams that flow from the west. The Damascus Basin lies within the Irano-Turanian phytogeograhical region. The vegetation in the area has become degraded because of overuse of the natural resources. Tell Ramad is situated farther to the west, outside the area formerly occupied by the ancient lake. In these higher elevations the natural vegetation is typical of the Xero-Mediterranean almond-pistachio forest steppe. Tell Ras Shamra is located in northwestern Syria, close to the Mediterranean coastline (van Zeist and Bakker-Heeres 1984:151-153). The site lies within the Eu-Mediterranean forest region.

**Fig. 1. Map of Syria with locations of the archaeological sites.**

Occupation at the five sites spanned the time during which it is thought cultivation began. The periods represented at the sites are also those for which there is the first evidence of domestic crops and signs that cereal-based agriculture spread throughout the Levant. The published data for the sites were in the form of lists of plant taxa, with numbers of taxa recorded per sample and per occupation phase. The authors undertook simple numerical analyses and made comments based on subjective assessments of the data sets about the relevance to early cultivation of the differing proportions of crops and wild species (van Zeist and Bakker-Heeres 1982:234-241, 1984:167-169, 1986:192-194).

From the outset the aim of this investigation was to look for patterns and trends in the archaeobotanical data that might reflect developmental changes associated with the control and use of plant resources through time. Multivariate statistical analysis was used to investigate any covariational relationships between the taxonomic composition of samples and chronological phases.

Multivariate analysis is described succinctly by Lange as a means by which for large data sets:

> "Redundancy of information is summarised, noise is reduced, outliers can by identified and relations are brought to light." (Lange 1990:41)

Fig. 2. Radiocarbon dates of the archaeological sites in Syria.
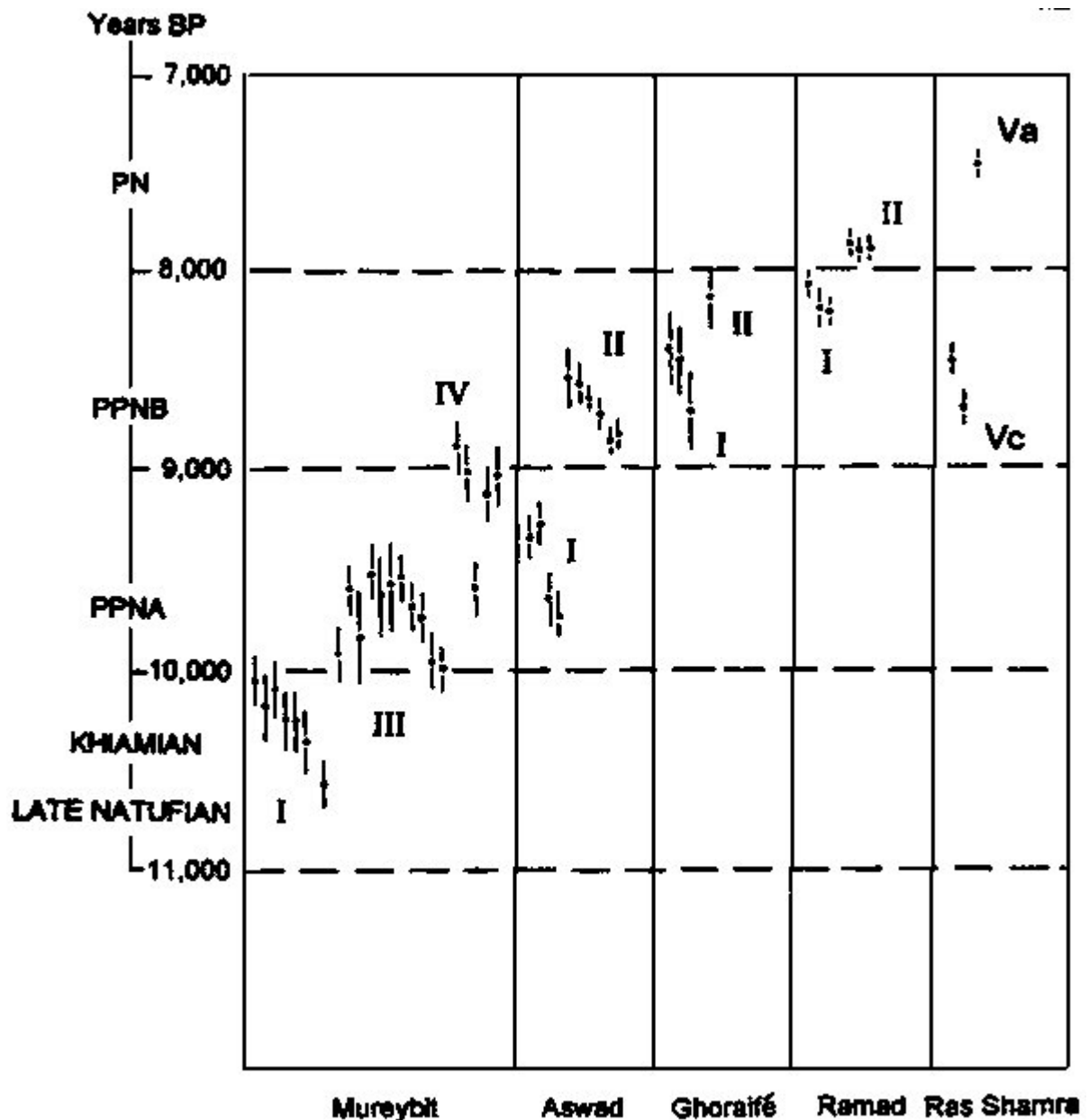
In this study it was relevant to use simple correspondence analysis as the multivariate technique, it being an analytical method ideally suited to data of the abundance-type (the data sets for the sites in question were large, comprising counts of over 200 taxa from 244 samples). Many statistical analyses are applicable only to data with a normal distribution, which data of the abundance-type seldom have, but correspondence analysis makes no assumptions concerning the distribution of variables in the data set. Of importance to this study also was the fact that correspondence analysis is symmetrical with regard to the samples and taxa, i.e. they are analyzed in the same multidimensional space and the results can thus be shown on the same plots (Høiland-Nielsen 1988:37). Lange (1990:43) comments:

> "In graphical form the results of a Correspondence Analysis bring out the position of each sample relative to all other samples and to all the species, and of each species relative to all other species and to all the samples in the analysis."

Exploration of the data sets using correspondence analysis was essentially an exercise in 'pattern searching', looking for any meaningful grouping of samples from the sites by phase or geographical region. The analyses comprised a long series of progressional steps, each step being based on the outcome of the previous one, and at each stage the data sets were refined (e.g. sites were included or excluded where appropriate, non-frequently occurring taxa or groups of taxa were eliminated, etc.) in order to define more clearly any observed patterns. The most informative analyses, i.e. those which produced the most meaningful patterns of clustering of samples within site groups and phases, were those which used the composition of the wild/'weed' taxa only (i.e. the 'crop' components were non-discriminatory; in this paper all the discussions refer to analyses of the composition of the wild/'weed' taxa in the archaeobotanical assemblages). Where there were obviously demarcated clusters of samples it was an indication that those samples within a cluster comprised similar suites of taxa, and significantly different suites to those in other clusters. The term 'weed' is applied here with caution, given that for these periods and in these locations there is bound to be considerable ambiguity concerning the status of taxa that are now designated obligatory segetals.

Figure 3 shows a correspondence analysis (hereafter denoted CA) output plot for the wild/'weed' taxa in the samples from the three sites in the Damascus Basin: Tell Aswad, Tell Ramad and Tell Ghoraifé. The plot shows that the samples fall into three distinct groups. In the plots CA the strongest separation will appear along the first principal axis (horizontal) and then along the second (vertical), thereafter along axes 3 and 4 (all plots in this paper show the first two principal axes). The Tell Ramad samples are separated from those of Tell Ghoraifé and Tell Aswad along axis 1, and the latter two sites are separated along axis 2. This indicates that the taxonomic compositions were significantly different in all three sites (although the sites have a majority of taxa in common). The implication is that the archaeobotanical record has preserved a Vegetational fingerprint', presumably as a result of diverse plant-related activities which led to the transport and deposition of the different suites of taxa at each of the sites.

The sensitivity of the archaeobotanical record

Figure 4 shows a CA plot with two additional sites in the data sets; Tell Mureybit and Tell Ras Shamra, but in this case only samples dating to the Pre-Pottery Neolithic B (PPNB) period are included in the analysis. Again the samples from each of the sites form definable and distinct clusters: Ramad, Ras Shamra and Mureybit are separated from Aswad and Ghoraifé on the first principal axis, with further separation along the second axis (rather less clearly for the Mureybit samples in this plot). It seems, therefore, that - whatever the nature of the activities that led to the deposition of plants at the sites - they were repeated and consistent, such that the Vegetational fingerprints' were established at each of the sites within relatively short periods of time (e.g. a little over 1000 years for the PPNB).

Analyses run for individual sites showed even more clearly how the different phases of occupation were defined by the wild/'weed' taxa in the archaeobotanical assemblages. In the CA plot for Tell Ras Shamra (Fig. 5) the three phases of occupation are separated along axis 1 (to a lesser extent along axis 2). Further confirmation of the sensitivity of the archaeobotanical record is evident in this plot. An aberrant 'Halafian' sample appears to nestle among the Pottery Neolithic/Late PPNB clusters (i.e. it has a taxonomic composition characteristic of the earlier phases), implying perhaps that the archaeologist has assigned it wrongly to the latest phase. Of note is the apparent time trend in this plot, with the earliest phase (Late PPNB) at the extreme right hand side and the latest phase (Halafian) at the left.

Fig. 3. Correspondence analysis of the Damascus Basin samples for wild/'weed' taxa only, after taxa occurring in <10% of the samples have been omitted.
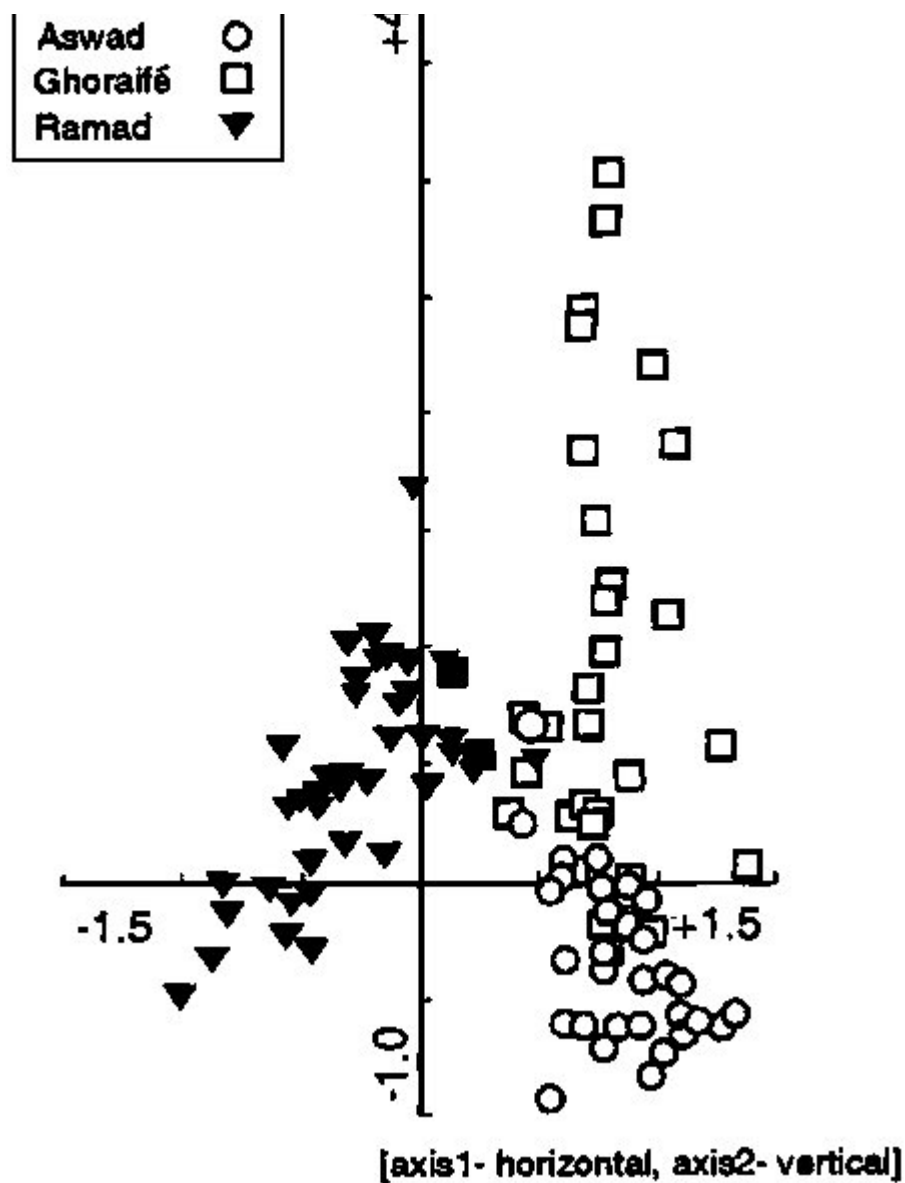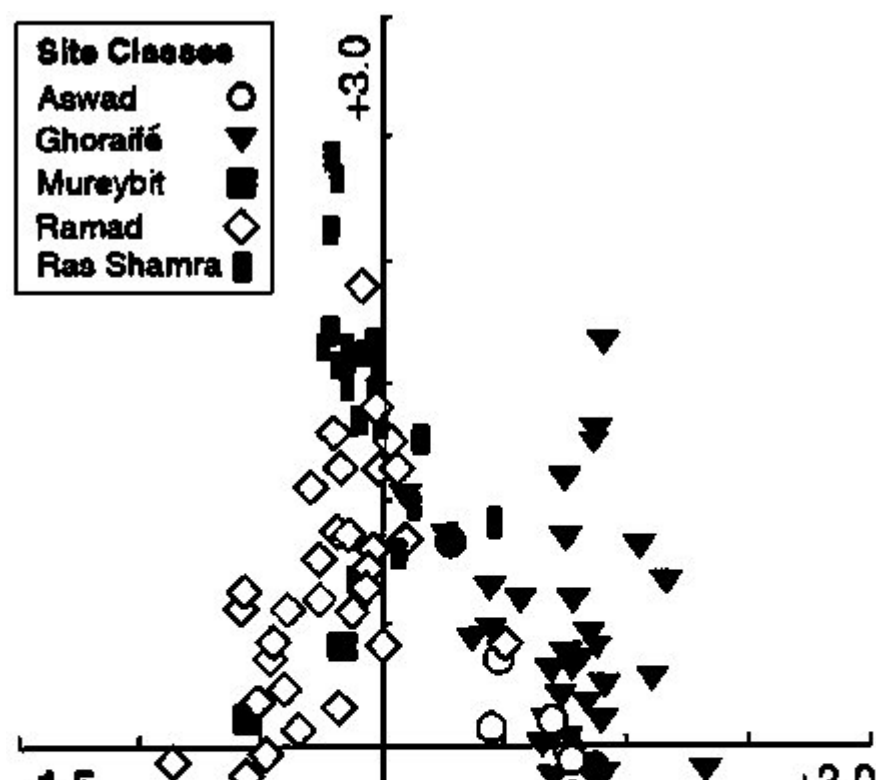
Fig. 4. Correspondence analysis of the Syrian Pre-Pottery Neolithic B samples for wild/'weed' taxa only.

Legend (top plot):
- Aswad ○
- Ghoraifé □
- Ramad ▼

Axis labels: -1.5, +1.5, -1.0, +1

[axis1- horizontal, axis2- vertical]

Legend (bottom plot):
Site Classes
- Aswad ○
- Ghoraifé ▼
- Mureybit ■
- Ramad ◇
- Ras Shamra ▋

Axis labels: +3.0, -1.5, +3.0

[axis1- horizontal, axis2- vertical]

It seems reasonable to propose that the 'vegetational fingerprints' are representative in some way of the floristic composition of the vegetation on land surrounding the sites. The differences between the sites and phases may reflect differences in the natural, undisturbed landscape or in the 'managed' land (i.e. the cultivated fields), or they may reflect either the relative availability of wild plant resources or the predisposition of people to choose certain taxa for use (or any combination of these possible explanations). It also follows, therefore, that the differences through time (coincidental with culturally defined boundaries) may relate to changes in any one of these aspects (whether caused by natural phenomena, e.g. climatic fluctuations, or by 'human-induced' factors). Presence of the wild/'weed' taxa on the sites would have been the result either of collection for use or of accidental inclusion with other plant material.

Interpretation of the 'vegetational fingerprints'

To shed some light on how and why the 'vegetational fingerprints' were established it was necessary to attempt to explain the patterns of samples in terms of the suites of plant taxa that characterized them. This involved classification of the plants; several different methods were attempted. The classification was considered to be successful (i.e. to be an appropriate explanation of the site or phase grouping) if it produced taxonomic patterning coincident with the relevant patterns of samples. The wild/'weed' taxa were put into categories according to (1) their growth habit (e.g. whether they were annuals, perennials, trees or shrubs, etc.), (2) the plant part which may have been used (e.g. whether leaf, stem, wood, fruit, flower or seed was useful), (3) the possible usage of plant (e.g. for food, fuel, construction, fodder, etc.), and (4) the plant ecologies (many other categorizations of the plant taxa could be appropriate but within the time constraints of this investigation only those listed could be applied). The most successful was the ecological classification. For this it was only possible to assign the taxa to very general ecological classes because of the limitations of nonspecific identifications and also the restricted information on habitat preferences in the published floras. The wild/'weed' taxa were grouped according to whether they grew in maquis, batha, field (those taxa which were obligatory segetals), wet and steppe/desert regions. The term batha refers to dwarf shrub communities in the Eu-Mediterranean zone where the aboreal cover has been denuded or has failed to develop (Zohary 1973:532).

Tell Mureybit and pre-domestication cultivation

The analytical exercise was perhaps most successfully applied in the case of Tell Mureybit. The CA plot (Fig. 6) shows the clear grouping of samples according to the periods of occupation. The samples from the Khiamian phase, an intermediate archaeological entity between Natufian and the PPNA, fall into two groups (van Zeist and Bakker-Heeres 1986:193-194). Interestingly, in this analysis, one allies closely with the PPNA group and the second allies with the PPNB.

Fig. 5. Correspondence analysis of the Tell Ras Shamra samples for wild/'weed' taxa only, after taxa occurring in <10% of the samples have been omitted.
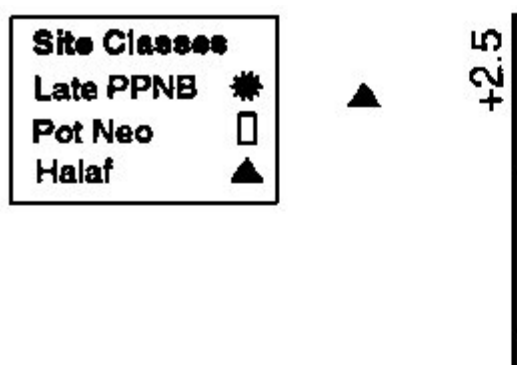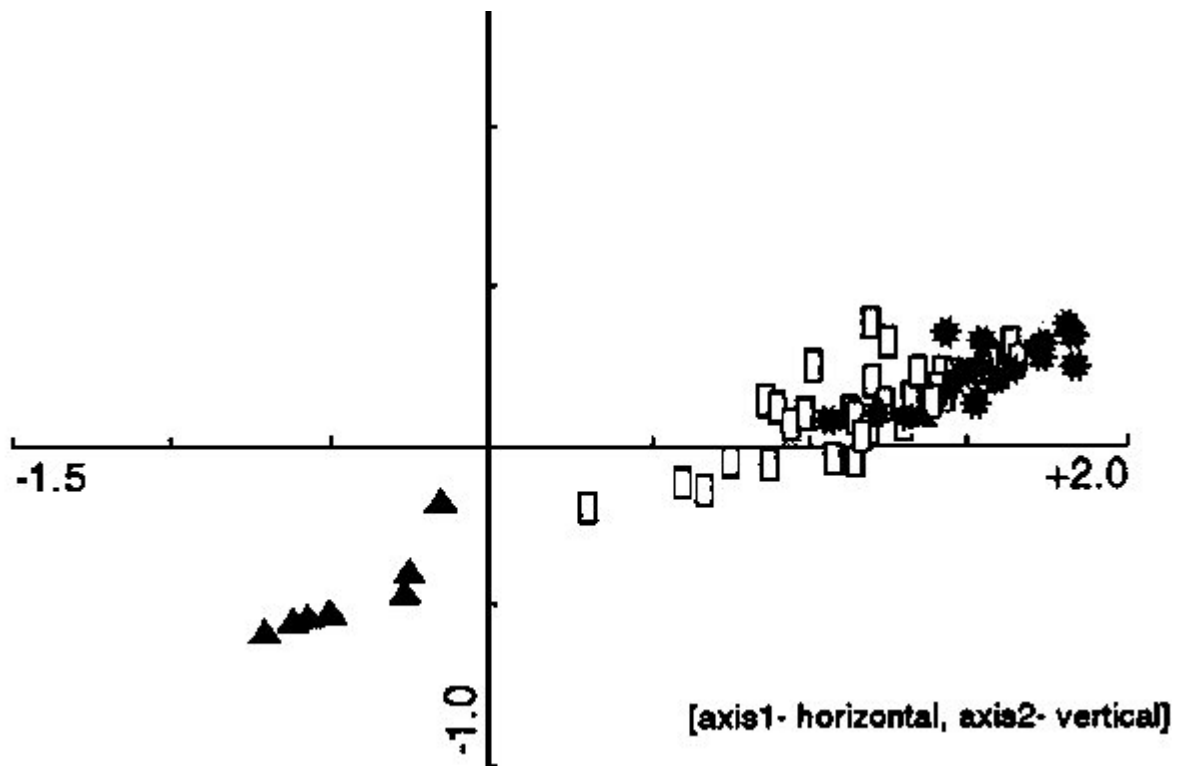
The easiest way to portray the ecological grouping of taxa within the samples was to use pie charts, where each pie chart represents a sample and the segments of the pie charts represent the relative proportions of the taxa in the different ecological groups. Figure 7 shows the pie charts for the equivalent sample plot, and there is clear patterning coincidental with that of the periods of occupation.

As discussed above, the suites of taxa are likely to represent in some way the floristic composition of the vegetation on land surrounding the sites, and so for Mureybit the dominant ecological groups for each period of occupation may be indicative of the most prevalent vegetation type at that time. If the assumption is made that 'human-induced' factors are at least as likely an explanation for the changes as the effects of natural phenomena, then the following interpretation may be appropriate. Wild einkorn wheat was the most commonly occurring 'crop' found at the site. A likely mode of transport of the wild/'weed' taxa to the site was as inclusions with the wild cereals, contaminants of the 'harvest'. It follows that the ecological grouping may reflect the composition of the vegetation in areas where the cereals were growing. So the dominance of 'wet-loving' taxa in the PPNA samples (for which high numbers of wild cereal grains were recorded) may indicate that at this stage the wild einkorn was growing on the alluvial margins of the Euphrates. A component of 'field' taxa appears in some of the PPNA samples and this may reflect the presence of disturbed ground that the 'weedy' plants would favor (as commented upon by van Zeist and Bakker-Heeres 1986:198). 'Wet-loving' taxa are not as apparent in the PPNB samples and this may be an indication that the wild cereals were growing on drier ground at this time. 'Field' taxa and taxa common in batha are represented in these samples. In this case the taxa common in batha were predominantly annuals, and it is this aspect of the group which may be relevant to the study. The presence of taxa from both ecological groups could be an indication of tillage, in preparation for the growth of wild cereals. The 'weedy' taxa would favor the newly opened ground, and there may have been an increase in the proportions of annuals as this growth habit is favored (as opposed to perennials) if the soil is disturbed in cultivation.

Fig. 6. Correspondence analysis of the Tell Mureybit samples for wild/'weed' taxa only, after taxa occurring in <10% of the samples have been omitted.
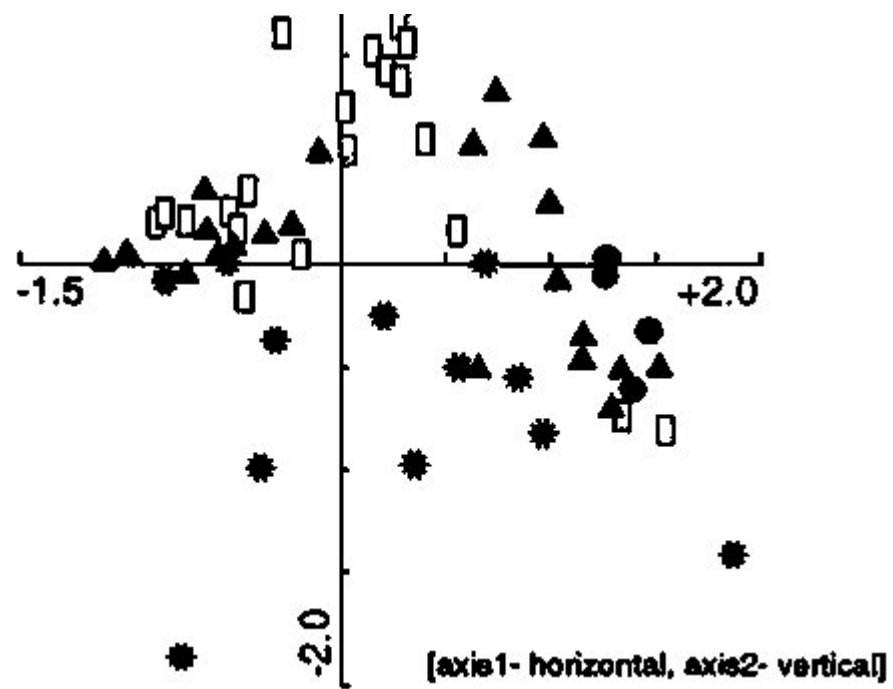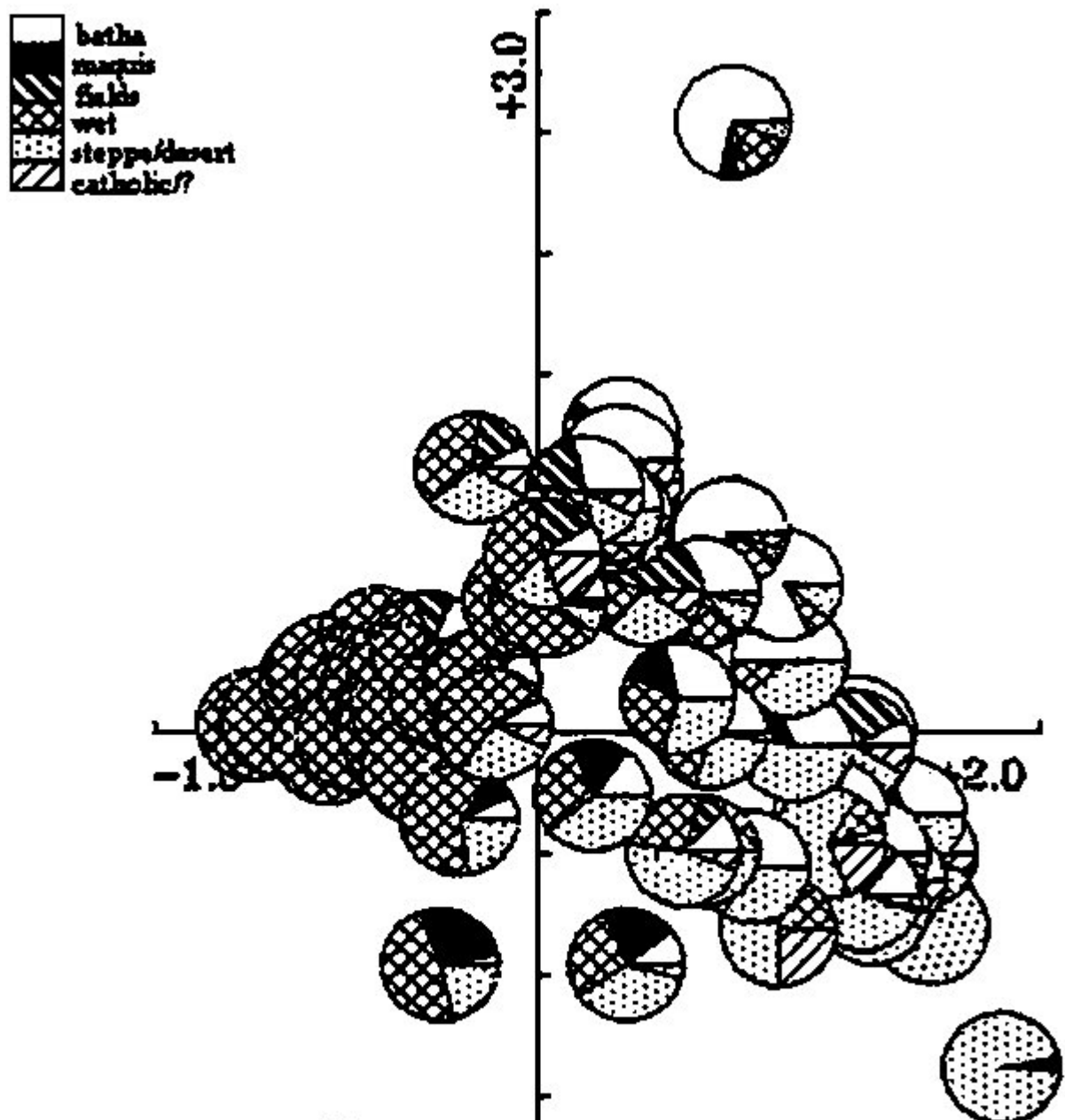
[axis1- horizontal, axis2- vertical]
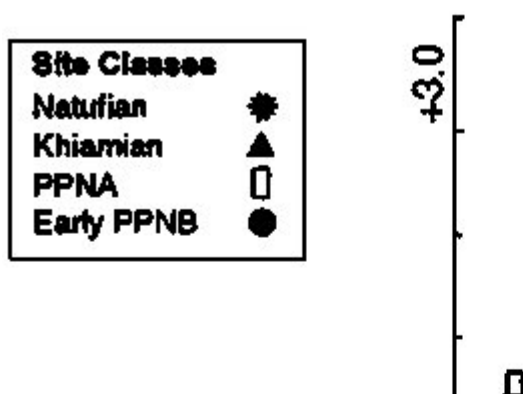
Fig. 7. Pie chart of the Tell Mureybit samples for wild/'weed' taxa only showing ecological categories.

Conclusion

It appears, therefore, that the application of correspondence analysis to the wild/'weed' taxa in the samples from Tell Mureybit, together with appropriate ecological classification of those taxa, indicates pre-domestication cultivation of wild cereals near the site (or in this case non-domestication cultivation, where the methods of land preparation and harvesting practices did not favor the selection of wild cereals with the 'domestic-type' genetic mutations, and so did not therefore result in the establishment of domesticated crops. It is proposed that the increasing energy applied to the land, in the form of tillage, causing interference and alteration of plant communities, is reflected in the archaeobotanical record.

Van Zeist concluded that the weed seed frequencies lent no support to the hypothesis of 'protoagricultural' practices and that the interpretation of the plant material must remain inconclusive (van Zeist and Bakker-Heeres 1986:198). I argue, to the contrary, that statistical manipulation of the numerical data in the form of correspondence analysis may allow pre-domestication cultivation to be recognized on early multiperiod sites such as Tell Mureybit.

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Pre-Pottery Neolithic A and Pre-Pottery Neolithic B Lithic Agricultural Tools on the Middle Euphrates: The Sites of Tell Mureybit and Tell Halula - J.J. Ibáñez, J.E. González, A. Palomo and A. Ferrer

Introduction

The study of the origins and first developments of agriculture must be approached in an interdisciplinary way, taking into account fields of analysis such as the identification of archaeobotanical remains, plant genetics, soil micromorphology, etc. Within this endeavor to gain an understanding of the characteristics of primitive agriculture, a fundamental aspect is provided by the study of prehistoric implements. New productive tasks demanded a marked technological change, which is at the very root of the economic transformations that then took place. It was necessary to innovate and to perfect tools used in the preparation of the soil and in the gathering and processing of crops. The study of tool culture is, consequently, key to gaining a knowledge of the development of agricultural techniques.

Analysis of the function of implements found at the sites of Tell Mureybit (J. Cauvin 1979), levels IIIa, IIIb and IVa, and from the sequence at Tell Halula (Molist 1996), has allowed us to identify some aspects of the development of agricultural techniques between the beginning of the PPNA (10th millennium BP) and the late Neolithic period (first half of the 8th millennium BP) in the middle Euphrates Valley. In this study we shall concentrate on two types of agricultural implement: sickles and hoes.

The morphology of sickles

The sickle is the tool characteristically used in cereal-based agriculture. Research undertaken by Anderson (1988, 1992) and Unger-Hamilton (1989, 1992) has provided interesting information concerning the use of these instruments, particularly during the early days of agriculture.

The main aspects that characterize sickles from this period are the shape of the shaft and the manner in which the pieces of flint were inserted into it. These two factors determined the way the implement was used and how effective it was. Natufian bone sickles are well documented, such as those found at Umm ez-Zoueitina (Neuville 1951), and at El Ouad and Kebara (Turville-Petre 1932). These are straight shafts containing blades of flint inserted in a parallel fashion.

Excavations at Tell Mureybit from PPNA discovered flint pieces used for cereal-harvesting consisting of straight blades that reveal a use-wear polish parallel to one or both edges of the piece. This shows that the pieces were inserted parallel to the shaft. One of the sickle pieces from level IIIa at Tell Mureybit is a broad blade of relatively large dimensions (135 x 42 mm) which carries the signs left by cutting cereal all along the edge, the traces being most intense in the middle and at the far end of the edge (Fig. 1). On the side opposite the blade the piece reveals a cortical back with a series of irregularities that were not removed by retouching. The distribution of marks and the shape of the back of the tool show that this piece was actually hand-held when used. It was, therefore, a harvesting knife, used to cut cereal stalks which would be held in the hand opposite to the one that held the knife. At this level of the site a limestone shaft turned up with a groove for the insertion of a flint blade (Anderson 1992). The shaft and blade together would constitute a kind of implement similar to a large-dimensioned blade. It is possible that apart from these harvesting knives there existed other tools distinguished by having one area for the insertion of the blades and another for grasping. Some of the blades showing traces from harvesting are quite long, between 8 and 12 cm, which indicates that the shaft into which they were inserted had to be straight. Nevertheless, the greater part of the sickle components are smaller, between 3 and 5 cm. In these cases it is difficult to ascertain whether the shaft they were inserted into was straight or bent.

Fig. 1. Flint blade with marks from harvesting, probably used without a shaft and held by hand. Level IIIa at Tell Mureybit, PPNA. Drawing: A. Deraprahamian.
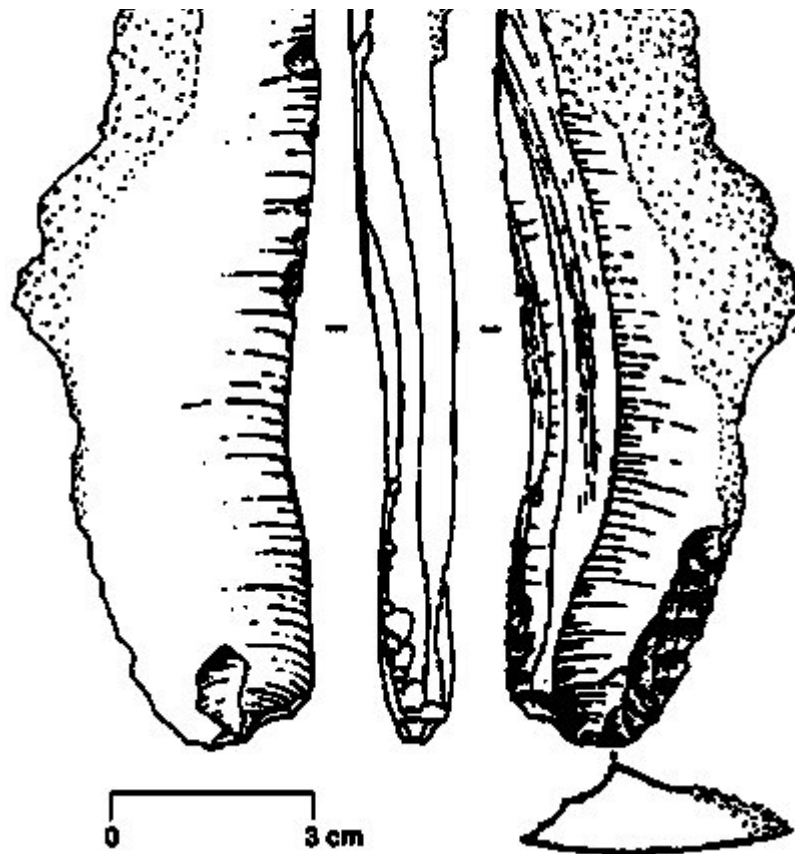
The data obtained from the sickle pieces found in the old and mid-PPNB levels at Tell Mureybit and Tell Halula point to systems of shafting similar to those observed in the PPNA (Fig. 2). The morphology of the pieces and the distribution of the use-traces are similar to those from the preceding period. Long blades exist that must have been inserted into straight-shafted sickles, alongside others of lesser size that could be used in both straight and bent shafts (Fig. 3).

Fig. 2. Mid-PPNB sickle elements at Tell Halula.

Fig. 3. Late Neolithic sickle elements at Tell Halula.
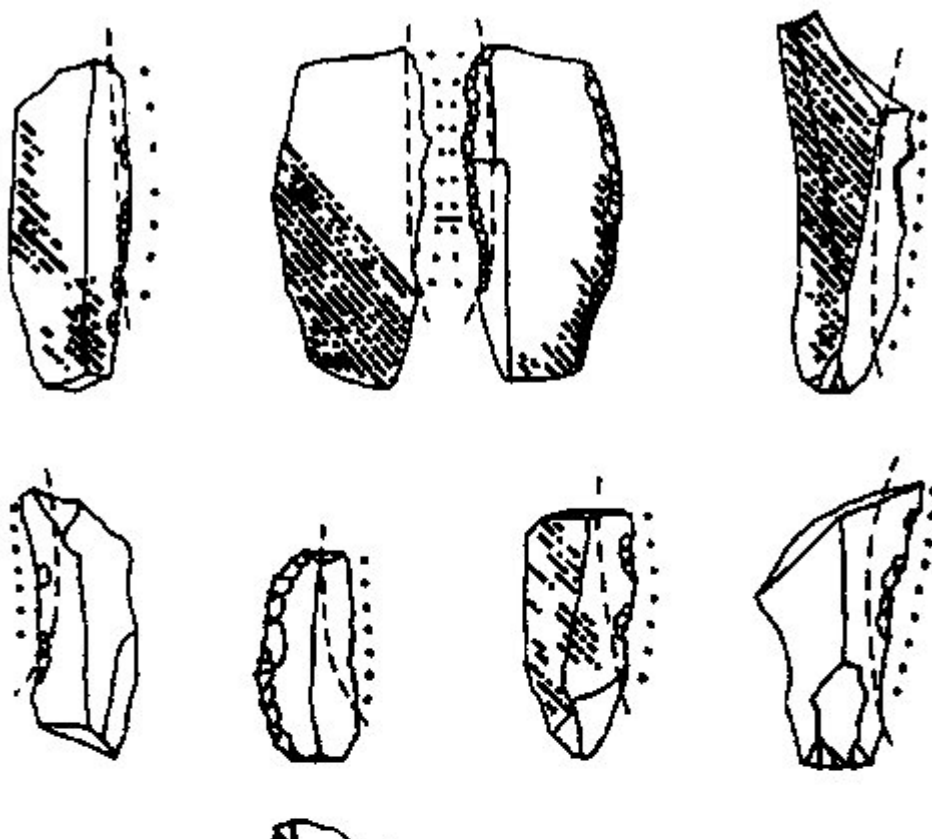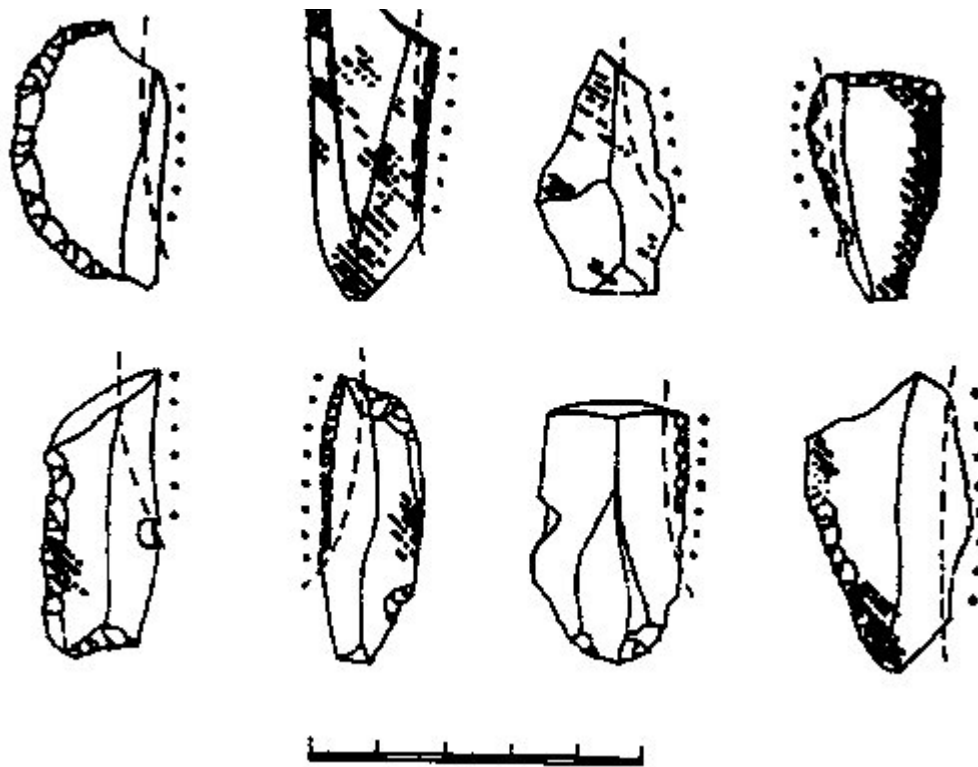
However, from the Late PPNB at Tell Halula important changes can be observed in sickle morphology. At this point distributions of traces appear in an oblique position, relative to the edge. During the late Neolithic period, the sickle elements with traces in oblique disposition amount to 70% of the glossed tools (Table 1, Fig. 4). Fractured blades were inserted obliquely into the shaft. Since the sickles were made up of various insertions, the outline of the edge was toothed. Moreover, the distribution of bitumen residue used for hafting the pieces with a shaft, very common in the sickle pieces from the site (Table 1), shows that it is a question here of curved shafts, rather than straight ones. The curvature of the shaft would draw an arc with a radius of around 10 cm. The curved sickle with oblique insertions also has been identified on the site at Tell Aswad, in PPNB levels (Cauvin 1973). This type of sickle continues to be dominant in the late Neolithic period at Tell Halula, although it must be pointed out that both in the Late PPNB and in this period some sickle elements show use-traces which are parallel to the edge (Table 1).

While we can state that the use of oblique insertion began, at least in Tell Halula, in the Late PPNB, it is more difficult to situate chronologically the beginning of the curved shaft, since some of the pieces from the PPNA at Tell Mureybit and from the PPNB at Tell Mureybit and Tell Halula could have been inserted into this kind of shaft. The sickle from the cave at Nahal Hemar, from the second half of the 9th millennium BP, has a curved shaft with parallel pieces (Bar-Yosef and Alon 1988). From the 8th millennium BP onwards, curved sickles from Çatal-Höyük VI-V and the later ones from Hacilar VI-II are known (Mellaart 1963, 1970; Cauvin 1983).

The change in sickle shape, evidence of which dates at least from the Late PPNB at Tell Halula, must have meant an important transformation as far as the cutting motion and its productivity were concerned. The harvesting experiments we have carried out with straight and curved-shafted sickles, whether with parallel or oblique insertions, have revealed the peculiarities of the work associated with each kind of implement. The harvesting work was done in Zuheros (Cordoba, Spain), where einkorn (*Triticum monococcum*) is still cultivated in the traditional way (Peña-Chocarro 1996), i.e. it is harvested using sickles. The experience of harvesting which the farmers in the area transmitted to us allowed us to understand the relationship between the shape of the tool and the technical movements which the cutting work requires (González *et al.* 1997). With the straight shafts one has to gather the stalks with one's free hand, then make a series of tangential cuts on the bunch of stalks. However, the curved shape of the sickle allows one to group together the stalks that are to be cut, using the tool itself. The farmers of Zuheros emphasized the importance of this movement, which they literally describe as 'calling the stalks'. They are grouped together with the sickle, held in the free hand and cut with the tool. With this technique it is possible to carry out the task of gathering the stalks by moving the sickle inwards, and to cut them by making the opposite movement with the tool. Thus, a continuous technical movement is made that allows the harvesting to be done with greater agility.

Moreover, from our field experience, we observe that with the use of oblique insertions, which produce edges with a toothed outline, a certain transverse component is offered when cutting which makes it possible to harvest bunches of stalks of a greater size.

In conclusion, the oblique insertions and curved shape of the sickles must have meant a certain advance in harvesting tasks, since they must have been accompanied by changes in the technical movements used in this work, with a corresponding increase in productivity.

Use-wear traces

As regards the characteristics of the traces left from harvesting, microscopic observation has shown that throughout the sequence at Tell Mureybit and Tell Halula the use-traces tend to be more and more intense with a more striated use-wear polish. These two aspects had already been mentioned by other researchers (Anderson 1992; Unger-Hamilton 1992). The greater intensity in the use-traces must be placed in relation to the greater importance of the work in the more recent period. The presence of more grooved use-wear polishes has been explained by cereal-cutting, the cultivation of which meant tilling the land. The cereal stalks would be impregnated with dust from the worked soil, which would produce the striations (Unger-Hamilton 1989, 1992). Nevertheless, this hypothesis has been rightly questioned (Anderson 1992; González *et al.* 1997). The presence of striations in the polish is connected with: (1) the degree of dampness in the material being worked on, (2) the presence of abrasive elements in the working context, and (3) the intensity of use. The lower the degree of dampness (1), the greater the presence of abrasive elements (2) and the greater the intensity of use (3), the greater the number of grooves that will appear in the polish. In our opinion, the increase in striations in the tools of the most recent periods must be situated in relation to:

- the cutting of ripe cereals, which means a lower level of dampness in working conditions

- the increase in the tendency to cut the plant from below, near the ground, with the aim of making use of the straw, and

- more intense use of the tools.

Why sickles?

In the Near East, flint implements were used for the harvesting of cereals from the Natufian period. However, cereals can be gathered in different ways without resorting to cutting. Wild cereals can be pounded with a stick and the grain gathered in a basket, or can be harvested by hand, as demonstrated by ethnographic examples (Harlan 1992; Hillman and Davis 1992; de Moulin, pers. comm.). Hulled cereals under cultivation can be gathered by hand, or by using systems involving nipping the ear, as is practised with mesorias (Sigaut 1978; Peña-Chocarro 1996). So, one has to ask what the motive was that led to the generalized use of the sickle for this task. Some authors have related the use of the sickle to the need to make use of the straw (Sigaut 1996). In this way, harvesting with sharp implements would be related to contexts where there is a need to use the grain and the straw. Nevertheless, it is not reasonable to suppose that during the Natufian and the PPNA the need for straw for construction and the manufacture of objects was as great as might be suggested by the number of sickle pieces encountered in the levels corresponding to these periods. In fact, in the adobes of the PPNA (Tell Mureybit, Jerf el Ahmar) fragments of cereal stalk are not found, since only the chaff from the ears was used. Stalks begin to be in evidence in the adobes from the PPNB onwards (D'jade, Tell Halula) (Hillman and Davis 1992; Anderson, pers. comm.). On the other hand, in some contexts involving domestic cereals, when sickles are used a cut is made in the stalk close to the ear, with no intention of making use of the straw. In Egyptian drawings in the *Book of the Dead,* in which harvesting tasks are depicted, it can be observed that the stalks were cut with sickles some 20 cm below the ear. In the present day too, in Zuheros, einkorn is harvested employing a high cut, thereby avoiding contact with the thistles that make their appearance in the fields like weeds, and thus making the worker's job more comfortable. In this case the exclusive aim is to obtain grain, since the straw is not used.

Fig. 4. Lithic implement probably used as a hoe. Mid-PPNB at Tell Halula. Drawing by A. Deraprahamian
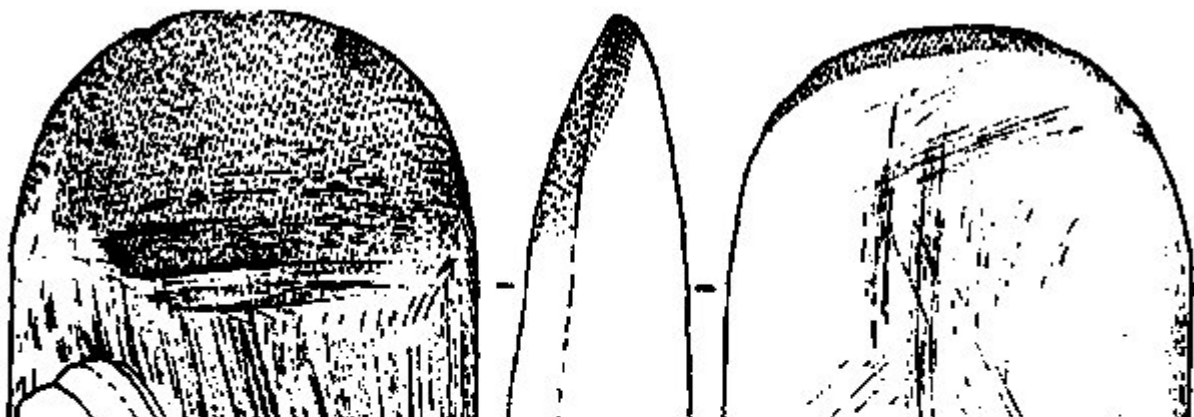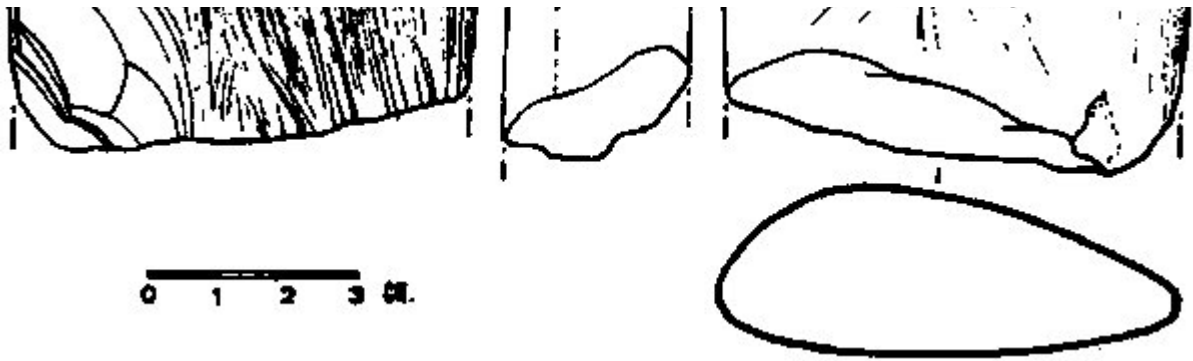
Table 1. Technical characteristics of mid-PPNB and late Neolithic sickle elements at Tell Halula.

	Late Neolithic		Mid-PPNB	
	Number	%	Number	%
Flaking type				
Unipolar	37	67.3	27	19.1
Bipolar	14	24.5	90	63.8
Other	4	7.2	24	17
Type of blank				
Blade	40	72.7	141	100
Flake	12	21.8	0	0
Indeterminate	3	5.4	0	0
Type of flint				
Black	5	9.1	58	41.1
Brown	48	82.3	83	58.8
Distribution of gloss				
Indeterminate	2	3.6	0	0
Parallel	11	20	141	100
Oblique	39	76	0	0
Bitumen				
With	22	40	56	39.7
Without	28	50.9	85	60.2
Indeterminate	5	9.1	0	0

The technical justification for the use of the sickle, therefore, resides not only in the need to make use of the straw; there must also be other reasons to justify its use, also including when the intention is exclusively of a grain-gathering nature. The ethnographic work we have carried out in Zureda (Asturias, Spain) and Zuheros (Córdoba, Spain) allows us to suggest some hypotheses in this regard.

Zureda is in Asturias, in the north of Spain, a region with a damp Atlantic climate. Spelt (*Triticum spelta*) and emmer (*Triticum dicoccum*) are cultivated in these parts and mature at the beginning of September. Harvesting is carried out with mesorias, an implement consisting of two wooden sticks between which the ears are pincered and then pulled off in a tugging movement (Sigaut 1978; Peña-Chocarro 1996). The ears fall into a basket while the straw remains in the field. Why are sickles used for harvesting in Zuheros whereas mesorias are used in Zureda?

In Zureda we were able to verify that harvesting with simulated Neolithic sickles was up to three times faster than the gathering process using mesorias. However, with the sickle system the workload is reduced, since it is not necessary to separate the straw from the ears. In contrast, in Zuheros, threshing work is relatively expensive. What can have led to choosing between these two options in each context? In Zuheros (Andalucía) which has an arid mediterranean climate with very hot dry summers, the available time during which harvesting has to be done is limited to about a week. If the reaping work is delayed, as the farmers told us, the wheat becomes too dry and the heads fall down on the ground when cut and there is a loss of production. In Zureda, on the other hand, in a damp Atlantic climate, harvesting can be drawn out for up to three weeks without the losses seen in more dry

areas. Moreover, the fields are of relatively small dimensions. So, in Zureda they opt for a technical solution that involves prolonged working in the fields because the atmospheric conditions and size of the fields allow this. In Zuheros harvesting must be carried out in a short space of time, for which it is necessary to use a tool that allows the work to be completed quickly.

It is assumed that the relatively dry atmospheric conditions in areas of the Near East at the beginning of the Neolithic period meant that the time available for gathering a wheat crop was relatively short. In the experimental fields at Jalés, the harvesting time available for wild wheat (*Triticum boeoticum*) is very limited, actually less than a week (G. Willcox, pers. comm.). This is the interval of time during which the cereal grain is physiologically mature but the plant is not yet completely ripe, and it is consequently possible to cut it without losing too much grain. During periods when the need for cereals was low, it was possible to revert to slower or less productive systems of harvests (Hillman and Davis 1992) but once cereal exploitation increased, a reaping implement had to be chosen that would exploit work time in the fields to the fullest, as is the case with the sickle. Thus, the technical value of the sickle would be not just as a tool to obtain straw but also a highly efficient implement at harvest time. Once the maximum amount of cereal had been gathered in the minimum time possible, the cereal could then be processed further on the settlement at leisure.

Technical characteristics of sickle elements

The study of the technical characteristics of sickle elements found at Tell Halula has allowed us to pinpoint certain changes throughout the sequence. At no point do polished pieces become dominant among the retouched implements (Table 2). During the Middle PPNB, the most numerous retouched tools are the tips of projectiles, and in the late Neolithic, retouched flakes and blades.

During the Middle PPNB, a form of bipolar knapping was used, and this made it possible to obtain blades, some of which were used as sickle components. In the majority of cases these blades were used without retouching. In the late Neolithic the knapping was unipolar, and medium-grain flint, with worse cutting qualities, was most commonly used (Table 1). In this period, not only blades but also stone flakes were used as sickle elements.

Both in the Middle PPNB and in the late Neolithic, 40% of the sickle elements reveal residues of a gluing substance that had been used in fixing the elements into the shaft. However, on other types of implements (points, scrapers and bores) there are no such traces, which either means that these other tools were used with no shaft or that systems of fixing into the shafts were used that did not require the use of a gluing substance.

Hoes

Apart from sickles, during the Middle PPNB at Tell Halula we have found another kind of tool which we believe to be associated with farm work. It consists of extended pieces worked in limestone, displaying an active edge at one end. A dozen of these objects were found in the Middle PPNB layer of this site. The functional study of these tools is in progress, but the results obtained to date are sufficient to justify the following preliminary remarks. The stone from which the objects were made is relatively soft which enabled them to be shaped using flint tools. At a first glance one can see the striations left by such tools in the manufacturing process.

The fundamental morphology of the pieces, of an axe or adze-type, suggests percussion work. However, the stone they are made from is relatively soft, therefore its application would not be effective on materials of a consistency such as wood or bone. Moreover the active edges are relatively blunt, which provides another argument to rule out work on the above-mentioned materials.

On one side of the active edge a black layer can be seen. It was debated whether this might be the residue of the substance worked on which had stuck to the tool. On some of the pieces it was evident that use has left partial abrasions on that layer, especially in the areas nearest to the edge from which it was concluded that the layer was added prior to use. One of the pieces, whose edge was not used intensively, clearly reveals the way in which the layer was attached (Fig. 4). The edge of the object was dipped into a black liquid so that one of the sides became substantially impregnated, whereas the other was only affected in the form of a narrow strip stuck to the edge. The position of the black layer and the small black drops on the objects that can be observed with a magnifying glass reveal the liquid nature of the black product before it was impregnated. From the appearance of this product, it is very likely that the substance is bitumen.

The use marks indicate that the tool was used for a percussion action. In two of the four objects studied the edge is partially fractured from impact use. One of the pieces was used despite the break. Moreover on this same piece several microscars due to impact also can be observed. Both the fracture and the scarring have been subject to partial abrasion by later use. Apart from fractures and microscarring, use of the tool left abrasions in the active area, as can be seen in the rounding of the edge and the use-wear polish on the active part, particularly noticeable on the side with the black layer.

Table 2. Retouched tools from mid-PPNB and late Neolithic at Tell Halula.

	Mid-PPNB		Late Neolithic	
	Number	%	Number	%
Points	376	27.5	167	11.7
Glossed tools	141	10.2	55	3.8
Burins	188	13.6	119	8.3
Scrapers	116	8.4	98	6.9
Retouched blades	289	21.0	406	28.5
Retouched flakes	0	0	527	37
Pointed blades	62	4.5	0	0
Perforators	20	1.6	7	0.5
Other	181	13.1	46	3.2
Total	373		1425	

Consequently, we are dealing with percussion work such as that performed by an adze, as demonstrated by the presence of use-marks which are more intense on one side than the other. The material cannot have been hard but must have been abrasive, and the tool would have entered deep into it. These being the characteristics, our view is that the material being worked on must have been the soil. These tools would work like a hoe. What function would the black layer (very probably composed of bitumen), which appears on one of the sides of the active edges, perform? We have established that the black layer and the most intense abrasion marks are present on the same surface. The layer of possible bitumen would be aimed at reinforcing the resistance of the surface of the tool to abrasion from the earth. Indeed, the limestone from which the tools are made is quite soft. Moreover, bitumen offers enormous resistance to traction and abrasion. It is spread over one of the sides, since in hoeing one of the sides of the edge penetrates the earth and is therefore subject to abrasion.

Despite the protection afforded by the bitumen, use must have considerably altered the state of the active part of the tool, since the edges of the pieces show marks of reconditioning in the form of scraping with lithic tools. This reconditioning work would involve the active edge being impregnated with a new layer of bitumen.

Following the above assumptions we have designed an experimental program to test the efficiency of the tool and to compare the marks left by the experiment and the archaeological ones. We must state that the experimental work done until now is of a preliminary nature, and was carried out in Spain. Although we used limestone taken from near the Tell Halula site to make the experimental tool, we are aware that this limestone is softer than that which was selected for the archaeological tools. Also, the hoe was used on farming lands in Vizcaya (Spain). Therefore, the experience will have to be repeated in autumn of this year at Tell Halula, during the excavation season. Despite the preliminary nature of the experiment, it has produced interesting results. Once the piece had been made, using percussion and scraping with flint blades, bitumen was added to the active side. To do this the bitumen was heated until it became liquid and then the edge of the tool was dipped in it, with the active side facing downward. The piece was fitted with a wooden elbowed shaft and used to work the land, to clear away the vegetable growth on the surface and subsequently dig up the earth. The tool showed itself to be efficient for this task.

In our opinion, from the data presented so far it can be considered highly probable that these tools were used to work the land, but were they used for farming tasks? The houses on the site are made from adobe, in which case they might well have been tools for extracting the clay with which to make the adobe. However, one factor leads us to believe that they were more likely to have been used for farming work. The layer of bitumen and the abrasion marks indicate that the working angle of the tool was very low. This working angle is more apt for work that involves digging over the surface of the earth than for deep digging work, where the implement needs to strike the earth in a more perpendicular way.

Up to the time of writing, no mention has been made of the existence of tools for working the land in such ancient periods. Nevertheless, a number of signs seem to indicate that it was during the PPNB that the hoe made its appearance as a tool for that purpose. On several PPNB sites in the Zagros area, limestone implements of a very similar nature to the ones found at Halula have cropped up (F. Hole, pers. comm.), and these may have had the same function. At the PPNB levels of the Beidha site, some tools have been found that are fashioned from the extremities of cattle bones. The active part, situated on the diaphysis of the bone, is manufactured by making a bevelled cut in the diaphysis. The active areas reveal microscarring, rounding, grooves and use-wear polish that would seem to imply that they had been used to work the land (D. Stordeur, pers. comm.). As regards later

periods, stone hoes have been documented on the Tello site, from the Obeid period (M.-C. Cauvin 1979) and perhaps also from the Moroccan Neolithic period (Bensimon and Martineau 1990).

Very few data are available to us concerning the characteristics of land-working tools in the early stages of agriculture. It is probable that, at first, wooden implements such as digging sticks or spades were used. However, as agricultural production intensified and the same fields began to be used year after year, it became necessary for the job of turning the earth over to be done more intensively, to mitigate the effects of the loss of productivity of the soil. In this context it would have made sense for the hoe to make its appearance, since it is a tool that allows the soil to be dug over more intensively and systematically (Sigaut 1978). Archaeobotanical studies carried out at Tell Halula (Willcox and Catalá 1996) point to the appearance of a wide variety and diversity of weeds alongside the crops. This evidence implies that continuous crops were cultivated in the same working fields. So, the appearance of hoes from the PPNB at Tell Halula, and probably also at Beidha, would reflect the growing intensification of farming work.

Conclusion

The study of tool culture among the Neolithic human communities provides information on the first agricultural techniques and implements. In fact, the development of the tools used reflects the growing importance of agriculture within the group economy between the 10th and 8th millennia BP.

During the PPNA, sickle material is relatively abundant. The generalized use of this implement for gathering wild cereals must have been motivated by a desire to get the maximum profit from this resource. Compared with other harvesting systems such as pounding with sticks or collecting by hand, the sickle made it possible to harvest more over a relatively short period of time. The speed of the work must have been a key factor when selecting the technical process for the exploitation of wild cereals, since the time period during which harvesting can be carried out is very short.

A development can be seen in sickle morphology, with a tendency toward greater working efficiency. It is difficult to establish precisely when curved-shafted sickles began to be used, though they were used, at least, in the Late PPNB at Tell Halula, and even somewhat before at Nahal Hemar. The adoption of the curved shaft and the appearance of obliquely inserted flint elements permitted the development of more continuous and efficient harvesting techniques.

Use-wear polish on tools used for harvesting, which becomes more and more intense and striated, reflects the progressive tendency to cut cereals when more ripe, as the process of domestication of these plants occurred. Reaping work progressively intensified, whereas in the more recent periods, ground-level harvesting would tend to become more important since it yielded a considerable amount of straw for roofing, cattle feed or bedding.

The data available so far seem to point to the existence of hoes during the PPNB. The intensification of agricultural work, repeated year after year on the same piece of land, would seem to imply an increasingly marked need for digging over the soil, and this was undertaken with the generalized use of hoes.

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History of Harvesting and Threshing Techniques for Cereals in the Prehistoric Near East - P.C. Anderson

Introduction

This paper looks at evidence for harvesting and processing methods from two periods: when wild cereals were used in archaeological sites, and after the appearance of morphologically domestic cereal grains. We discuss whether these data show 'agriculture' to be present and evolving, increasing in quantity across these periods, or whether agricultural techniques make a rather more sudden appearance in a defined context. The dynamics of change leading to agriculture are often depicted as bipolar: a progressive reversal over time in dependency on food from the wild vs. food obtained through cultivation, and in production of wild plant food vs. crops (Harris 1996). In Harris' model the "wild plant food procurement" stage is followed by a lengthy and widespread stage of "wild plant food production", encompassing the duration of the domestication process. Similarly, Hillman and

Davies (1992) present a model suggesting a specific behavioral pathway to domestication of the wild cereal population by a human group, which breaks down this phase into several theoretical scenarios of cultivation of morphologically wild cereals. However, like Harris, they assume that tilling of the soil and sowing, the same basic techniques as for domestic cereals, were regularly and increasingly occurring.

My experience of ten years or so of cultivation experiments harvesting wild cereals in Syria and Turkey, and cultivating them in France, indicates that agricultural practices described above may have been used in exceptional circumstances, but make little sense as habitual methods for wild cereal exploitation. Differences between wild and domestic cereals impose use of different effective exploitation techniques for each. Wild cereals with shattering rachis and uneven-ripening habits tend to re-seed spontaneously, as enough spikelets always seem to escape harvest to regenerate the stand, unlike domesticated cereals, which owing to their semi-solid or solid rachis, and even-ripening habit, need to be perpetuated by cultivation. What could be the reason for regular practice of cultivation of wild cereals, when they could be harvested year after year from wild stands, without sowing? It would appear that efficient, non-agricultural strategies of exploitation and management may well have been used over most of the time of exploitation of wild cereals, much as ethnoarchaeological data shows that management systems of wild plants important in the subsistence base today use intensive and often sophisticated exploitation patterns over very long periods, without cultivation (see Ertug, this volume). Nonetheless this point continues to be overlooked; for example, Sheratt (1997) reviews arguments for climatic change as important in precipitating 'farming' of morphologically wild cereals, but assumes this would be the chosen form of intensive exploitation of these plants. Leach (1997), however, has correctly emphasized the lack of agreement on terminology and concepts concerning agricultural origins and food production systems. Did an 'agricultural threshold' actually occur during the period of wild cereal exploitation, or rather only later in time, near the beginning of cultivation of morphologically domestic cereals?

Material and methods

This research uses data that show which techniques and tools were used to harvest and treat cereals from 12,000 to 5000 BP (see Table 1). Using a system of 'feed-back', we have moved between research questions dictated by archaeological material, experiments in the field, and interpretation of archaeological material from the field data. The archaeological material we studied consists mainly of stone (and rarely, bone) tools made at the sites, which potentially were (parts of) plant-working tools. Wood and other organic material, often forming the handle or the body of tools, is rarely preserved. Therefore overall structure of instruments must be deduced from traces of use, residues of adhesive, and other kinds of analogy derived from ethnographic and experimental data. Three basic categories of tools will be discussed here: sickles for harvest, and two other tools for post-harvest treatment or 'threshing'.

We have also checked pieces of daub and mud brick from structures in the sites, where available, for imprints of stem and glume fragments which would have been used to temper the clay. We have studied such data from about 40 archaeological sites from the Natufian to the Bronze Age in the Near East thus far, spanning the time from the first use of wild cereals, to village and urban agricultural systems (see Table 1 for examples), as part of an ongoing research program. Over the years we have used experimental copies of prehistoric tools (Anderson-Gerfaud *et al.* 1991), to harvest or to thresh, chop, etc. wild cereals, or domestic cereals, as appropriate, given the nature of archaeobotanical remains from the sites having yielded the original tools (Table 1). These experiments produce data concerning either the effect on plants and tools of a given process, or actual traces of use on the tool's active area. Such data are necessary to demonstrate ancient tool use. Initially inspired by Harlan's (1967) wild cereal harvesting experiments in Turkey, we have harvested stands of wild wheats and barley in Syria, in the Jebel Arab region in the south, and near Ain el Arab in the north, and wild wheat and rye in southeastern Anatolia.

We also planted a collection of wild einkorn wheat which was collected in 1986 from 'primary' stands in southeastern Anatolia, found near sites in Turkey where early cultivation of domestic einkorn occurred. This wheat formed the basis for eight years of experiments, carried out by myself and George Willcox, in southern France, Jalès, Ardèche region (Anderson-Gerfaud *et al.* 1991; Anderson 1992), in order to understand possible methods of exploitation for wild einkorn in prehistoric contexts. Morphologically domestic wheats and barley were also used in experiments, and here interpretations of tools and processes from the past were helped by observing traditional practices in present-day Syria and Turkey. Table 1 shows presence of three kinds of tools we identified, in relation to their chronological and archaeobotanical contexts.

Table 1. (Facing page) Cereal treatment methods from the Natufian to the Bronze Age. ina = Information not available.? = Presence not certain. Blank = Plant, tool or attribute not found at site. Square: wild cereal remains identified. Circle = remains of domestic cereal grains identified. Triangle: presence of sickle use for harvesting of cereals identified in site from use-traces on blades. Diamond: Evidence of threshing using tools identified in sites from use-traces. Solid diamond: Bronze Age threshing sledge with Canaanean blades (structure described in footnote C). Last column: from examination of remains

of mud brick or of phytoliths.

Most plant-harvesting and processing tools from archaeological sites are preserved in the form of flint blades (sometimes obsidian). If they show microscopic traces of use, they may be interpreted according to our experiments, which allow differentiation of the actual use of the ancient tools (motion, material, etc.). The tool surfaces are observed using reflected-light optical microscopy at 100 and 200 X (Keeley 1980) and compared with a large data bank of potential characteristic traces. These kinds of observations of wear traces in optical microscopy are sometimes supplemented by identification of residues of the worked material preserved on the tools.

The scanning electron microscope and microanalysis have often been used to identify residues on the basis of characteristic morphology and elemental composition (Anderson 1980; Stordeur and Anderson-Gerfaud 1985; Anderson-Gerfaud 1986; Anderson and Formenti 1996). Other methods, not discussed here, are increasingly used to identify organic compounds preserved as residues, particularly for finding what material was processed with querns and other 'groundstone' objects (Juan-Tresseras 1997; Formenti and Procopiou 1998). Here we discuss only tools which were part of instruments for processing cereals, excluding grinding and pounding tools, but these are only a part of the overall picture of tool use and activities at this time, which includes function for hunting and butchery, for harvesting reeds, or for making objects of skin, wood and stone (Anderson 1994a; Anderson and Formenti 1996), etc.

Discussion and results

Harvesting tools

Method of harvest and field situation

Beginning in about 10,000 BC or 12,000 BP, each site (with the exception of those from the 5th millenium BP) has produced data showing numerous examples of blades (Fig. 1), undoubtedly mounted in handles (Fig. 2), which were used for harvesting cereals. These form the first of three categories of tool function that will be discussed here, whose occurrence is shown in Table 1. Sickles were generally used to harvest by cutting groups of cereal stems, pulling the tool blade back through the stems toward the user, cutting near the ground (Fig. 3). A visible 'gloss' on the cutting edge of such tools, seen using the optical microscope, shows features characteristic of harvesting: smooth, bright surface traversed by fine, short scratches or striations, probably from contact with soil grains, aligned parallel to the cutting edge (Fig. 4).

Harvesting tools identified (Table 1) in each case provide positive evidence for the use-situation described above, as well as for harvesting cereals at a precise time in their ripeness, and where groups of stems occurred in a density of over 300/m^2, judging from our experiments. This is the density we observed of wild cereals growing in natural, rather pure stands in eastern Turkey and Syria (Fig. 5), only 30 km from a site in the North Euphrates basin where wild cereals were used. Wild cereals are uneven-ripening, and are most effectively harvested during a period lasting only a few days at a given altitude and latitude, when seeds are still unripe and top spikelets are just beginning to dry and shatter (Fig. 6). Blades in sickles, used for cutting plant stems at this phase of grain ripeness, developed the microscopic traces having a bright, smooth appearance, described above.

Fig. 1. Flint blade, with gloss on edge and use-traces from harvesting, from Syrian Neolithic site with remains of wild cereal. Scale = 1 cm.

Fig. 2. Reconstruction of sickle used in experiments to harvest wild cereals, with flint blades (e.g. Fig. 1), glued in a groove of a wooden handle using bitumen.

Fig. 3. Harvesting of wild wheat in stands in the Jebel Arab, Syria, using the experimental sickle (Fig. 2).

Fig. 4. Magnification (100X) of the cutting edge of a blade in sickle in Figures 2 and 3. Traces of harvest include smooth bright surface and short striations (arrows) oriented parallel to the cutting edge direction.

Fig. 5. Relic stand of wild wheat near Ain al Arab, Syria, about 30 km from D'jade, middle Neolithic site with wild cereal remains, which may have extended nearer sites at that time. Note its density and 'purity' (lack of adventices or other plants).

Fig. 6. Uneven ripening habit of wild einkorn wheat, showing shattering of upper spikelets of seed head, which escape the harvester and self-seed to spontaneously regenerate the stand the following year.

Fig. 7. Reconstructed use of a bone tool (see Table 1) to separate ears of domestic cereal (here, emmer

The polishing of the blade edge producing this appearance is influenced by the action of water as a lubricant, because at this time, stems are green to half-green, and still contain significant amounts of humidity, according to our measurements (Anderson 1992). The striations correspond to soil grains on stems rolling over the tool edge during harvesting use, as well as perhaps abrasion from silica phytoliths contained in the stem epidermis (Anderson 1980). The longer the use, the more microscopic 'polish', marked by scratches and striations, becomes visible. Using these criteria, seen on experimental sickle inserts we used from 5 to 15 hours, most sickle inserts from archaeological sites with wild cereals represent harvesting of over 20 hours, which cannot for various reasons be converted into an estimate of surface area harvested.

Although harvesting wild cereal with a sickle was unlikely to have been the only method used (pulling up the plant or pulling off the seed head being preferable methods in sparser stands or when the plants are ripe and shattering), it is the only one leaving behind recognizable traces of tools. This means that it is impossible for us to compare quantities of cereals harvested at different periods just by counting numbers of sickles found in sites. However, the presence of sickle inserts in nearly all the periods discussed shows that harvesting in the manner described above must have been a very common practice, as only repetitive actions carried out over a period of time would reach our levels of detection today, given selective abandonment patterns, preservation and recovery represented by the archaeological contexts.

The importance attributed to sickles and their use from the beginning, during the Natufian, is shown by the fact that the blades show standardized morphology, undoubtedly to ensure calibration of multiple blades assembled end to end in grooves cut in handles and glued with adhesives. Experimental attempts to use similar tools underline the importance of balance between components of the sickle if it is to function over long periods of time (Anderson 1994a, 1994b). Their presence shows that durable and efficient tools were used in the same technological process over millenia, representing a technological continuity, as well as attesting to harvest in dense stands, even during the time when archaeobotanical remains correspond to use of morphologically wild cereals.

Sowing and tilling

We observed that simple harvesting of natural stands (or of fields left to re-seed spontaneously) stimulates their growth. The idea that harvesting required re-sowing of grain to replenish the field is contradicted by experiments and observations in Syria showing that self-seeding was always adequate to produce a dense new field the following year, however efficient the harvesting was in taking grain (Anderson-Gerfaud *et al.* 1991). Therefore it is difficult to imagine how any cultivation of wild cereals could have been frequent and widespread enough to constitute an evolutionary phase of wild plant food production, as most models propose. Other exploitation patterns can involve intensive use and even displacement, however. We were able to harvest stands after they were moved to and planted in southern France from Turkey, without turning to annual cultivation to enhance their propagation. This could simulate a situation occurring during the Natufian or the Neolithic whereby wild cereals were taken from original stands, to be transplanted as a 'new' stand nearer human habitations, but without further need for maintainance by cultivation (planting, tilling) after their initial installation in the new area, particularly as various data show that sites are already sedentary at this time (Cauvin 1994).

Other data

Archaeological data presently available do not appear to resolve the question of whether regular cultivation of wild cereals occurred. Although hoe-shaped stone tools were found in sites where wild cereal grain occurred, study of traces of use shows they were used as adzes for woodworking, not for working the ground (Coqueugniot 1983). No tools for working the soil have been found for which the study of traces demonstrates their use, before irrigation contexts in the 5th millenium BP, such as Tello (Cauvin 1979), although a possible hoe made of limestone was found at Halula (Ibáñez *et al.,* this volume; excavations M. Molist) which nonetheless involves a domestic cereal context, not one associated with wild cereals.

Two persons who studied stone tool function by observation of microscopic wear traces - Unger-Hamilton (1989) and Korobkova (1994) - saw traces on harvesting tools that led them to deduce that cultivation (working of the ground) occurred as early as the Natufian. They claimed that the striation or scratching they saw on flint blades with traces of harvesting was caused by contact with soil which was loosened, by tilling of ground for cultivation of wild cereals, to an extent that affected the future plant stems during harvest one year later, in a different way from

plant stems of wild cereals growing in a stand. This theory was disproved by our experiments, where we harvested wild cereals on a larger scale, over both tilled and untilled ground in the same environment, as well as in various natural stands in the Near East, as described above. All of the above produced striations on the flint and obsidian tool edges, but amount or density of striations increased only the nearer the ground the tool cut and the longer it was used. Therefore no correlation was found as to whether or not the ground had been worked or the plants had grown in natural stands, which discounts striations on stone sickles as criteria able to address the question of whether or not pre-domestic cultivation occurred (Anderson 1992, 1994a, 1994b; Anderson-Gerfaud *et al.* 1991).

Pre-domestic cultivation has been postulated by some where seeds of plants found in archaeological sites along with morphologically wild cereal grains could be adventices or weeds brought in by soil disturbance, possibly representing tilling (see Willcox, this volume). Colledge (this volume) proposes that changes in macrobotanical remains may reflect changes in field composition. We believe that these correspond to spatial management and tending strategies, or occasional transplanting or displacement of wild cereals, as opposed to annual preparation of fields and sowing.

Unconscious selection toward domestication

Using calculations from genetic data and limited field trials, Hillman and Davies (1992) established that domestication could have occurred due to repeated use of particular harvesting and cultivation methods leading to an unconscious selection for 'domestic-type' mutants, the rare cereals with a non-fragile rachis hidden among the spontaneous, fragile-rachis wild cereal population. This is because the methods, harvesting with sickles (or by pulling up the plants), followed by annual sowing of the grains gathered that year and annual re-tilling of the previous year's field (or movement away from it), would have the effect of, first, selecting for all grains present of 'mutant-type' plants which do not spill grain, and leaving behind in the field grain spilled from true 'wild' cereals, and second, preventing mixing of this harvest, increasingly consisting of mutants, with earlier crops or with wild stands. In this way, if this occurred annually over 20-200 years, selection for morphologically domestic (non-fragile-rachis) cereal would occur; the length of time needed was later extended by Willcox's (1991) estimates from our experiments. Aside from the estimated duration of the process, these practices, including sowing of wild grain away from prior fields or tilling them under, would need to occur without interruption yearly, otherwise the selection effect would be erased and the domestication process halted.

It appears unlikely that the particular combination of practices described by Hillman is characteristic of contemporaneous sedentary groups for which archaeobotanical data are preserved, such as those in Table 1. Indeed, no site known today shows a sequence of wild cereal followed by domestic cereal remains. Thus domestication's significant and apparently irreversible impact on the evolutionary process may have actually involved an isolated occurrence of regular use of an unusual combination of methods, over a limited time, near the end of the period of wild cereal exploitation. If these practices were used by a group moving regularly with wild cereal grain, in such a way that they distanced themselves from former fields or natural stands, and planted only the products of its last harvest each year, their yearly harvests would constitute greater and greater amounts of 'mutant' domestic-type grain, leading to domestication of the cereal population (Anderson 1992; Hillman and Davies 1992). The domestic grain would then spread rapidly throughout the area, and our data have shown that new techniques and instruments for cereal-processing appear at this time, adding to harvesting tools.

Domesticated cereals: harvest

We consider that sickles, about the only remains bearing witness to harvesting methods, show technical and functional continuity throughout the period discussed here, because the harvesting motion described above for wild cereals continues throughout the Neolithic and beyond for harvest of domestic cereal (Anderson 1994b, 1994c) with changes which occur in sickle morphology, for example increased length of blades making up the edge, or more curvature of the handle (see figure in Table 1), which undoubtedly improved their performance. A difference is that the time of harvest is open to greater social choice, as the ripening pattern of domestic cereals will not involve disarticulation of the spikelets and grain loss over a relatively short period, although seed heads of einkorn and emmer have been seen to disarticulate when very dry (Miller 1992). The appearance of traces on the blades from sites with domestic cereal remains is more variable than those from harvesting of wild cereals, corresponding to the greater choice of harvesting periods (up until the plant is very dry and brittle) where there is more or less humidity in the stems, which we have seen affects development of the 'polish' traces. Otherwise, as a technical process, the motion and manner of use show no significant difference from the prior period, and for that matter, from harvesting motions with curved metal sickles we have seen used today in Syria and Turkey.

Domesticated cereals: threshing

Contrary to observations above concerning harvesting tools and their use, changes occur in technical processes and tools used for cereal treatment at the moment of exploitation of morphologically domestic cereals.

Furthermore, these new techniques and tools do not appear to result from a gradual evolutionary process having its origins in wild cereal exploitation, but rather, represent significant technical innovation (Anderson 1994c). Threshing, used here to encompass all treatment after harvest of the plant other than breaking and grinding grain, corresponds to adoption of agricultural processes in the context of the first morphologically domestic cereals. This is apparently related to the change of cereals to domestic morphology (semi-solid or solid rachis from fragile rachis) and to the need, using tools, to produce certain products on a large scale at the site, for dietary and technical purposes (i.e. threshed grain, long length of stems, chopped stems). Wild cereals shatter into spikelets as they dry in the sun, needing no special tools for separation of grain from stems, whereas morphologically domestic cereals do in fact need manual intervention of some sort to separate the seed head from the culm or stem.

A tool has been identified, associated with the earliest dates for domestication of two-row hulled barley in the Kermanshah region in Iran, from the 8th millenium BP, which was used to strip seed heads from stems. These peculiar bone tools have a notched, V-shaped working area produced on scapulas of sheep and goats (see Table 1). About 100 of these tools were identified, of which several were studied in detail for function and use-traces (Stordeur and Anderson-Gerfaud 1985). These tools show gloss in used areas within notches, on straight areas of the same edges which, under the microscope, showed gloss but also striations oriented radially in the notches and parallel to the V-shaped edges. These traces of use are sufficiently characteristic of a certain motion that the use of the tool was able to be narrowed down. Use-traces on the ancient tools (the striation pattern above, but also gloss, and silica phytolith residues from grasses/cereals identified on the tools) were reproduced on the modern, experimental tools by pulling groups of stems, after harvest, through the notched V in the tools, producing clean separation of seed heads from stems (Fig. 7).

Domestic hulled barley appeared to be the most likely silica-rich plant processed using this tool type of those found on or around the site, and experiments showed that many thousands of barley stems would have been processed by each tool to produce the high degree of use-wear observed on the tools found at the site. Also, experiments made it clear the tool was indeed for cereal treatment, not harvest, because harvesting of barley in the field did not create the same wear traces as those on the archaeological tools. Other tools of this shape have been seen by the author at Çayönü in Turkey and reported from Tepe Abdul Hosein, Iran, and study of their use-traces may verify they also had this use. Study of use-traces (Skakun 1993) showed that a very similar tool was used in Bulgaria during the Chalcolithic, or 5th millenium BP, perhaps representing a 'diffusion' of this tool use from the Near East over several thousand years as part of a toolkit associated with early domestic agriculture. Finally, a scapula with a shallower and narrower groove cut than for our archaeological tools is still in use today in Japan for stripping seeds (not whole seed heads) from sorghum after harvest (F. Sigaut and E. Takei, pers. comm.).

The threshing sledge or tribulum

Certain blades, associated with only morphologically domestic cereals, also show gloss, but under the microscope their traces exclude use for harvesting, as they show other features, e.g. abrasion and long deep grooves of comet shape, long striations corresponding to a continuous motion in one direction (Anderson and Inizan 1994), that are characteristic of use as inserts in instruments functioning as threshing sledges or 'tribulums' (Fig. 8). The latter have been described by several researchers who have looked at use of these instruments and traces on their flint inserts (Whallon 1978; Ataman 1992; Skakun 1992; Anderson and Inizan 1994; Kardulius and Yerkes 1996). Such wear is apparently due to contact, by dragging, with dry cereal stems and seed heads, but also with a threshing floor surface of clay or stone. This instrument achieves threshing of grain and chopping of straw on a threshing floor, and is pulled by various animals, depending upon the context - oxen, horses or donkeys. Its overall construction is variable, but today and in the recent past it usually consisted of joined planks forming a board, with cutting elements of stone or metal inserted into the surface of its underside by hammering or gluing into holes, grooves or slots. Tribulums or threshing sledges, of various dimensions, have been used until recently (or are still used) throughout the Mediterranean region. Often the instrument is weighted during use by a person or stones.

The tribulum, armed with anything from 50 to 2000 fragments of stone on its underside (Fig. 9), is pulled around in a circle over the plant material, which for hulled grain breaks up the seed head into spikelets or actually releases the grain from naked cereal, as well as chopping stems into fragments (Fig. 10). All this material is then separated by winnowing and used for various purposes. Today, as in the past, these uses include temper for mud brick (attested to in the past from imprints or phytolith remains from stems in remains of clay walls of structures, see Table 1, last column). Other uses include food and bedding for animals, fuel, etc. Obviously threshing of grain accomplished by the instrument is essential to both human and animal food, but arguably this can be accomplished by any means of producing pressure and friction, such as trampling with animal hooves. The threshing sled, armed with sharp stone, would be important in chopping of straw for various uses.

Our clearest archaeological picture of the use of this instrument is for sites from the Bronze Age in the Levant

(Table 1, second-last column). However, according to cuneiform texts describing the instrument of this time in Mesopotamia (Anderson and Inizan 1994; Civil 1994; J.-P. Grégoire, pers. comm.), it shows major differences with the construction of the present-day tool, involving an assemblage of planks or boards, because it was made like a raft, of logs of small diameter which were assembled by lashing with leather straps, with bitumen used to glue the blades between the interstices in the logs (Fig. 11). The blades with traces characteristic of use as inserts dating from the Bronze Age (Fig. 12), are large, purposely fragmented Canaanean blades which are standardized in width and thickness, and for which the hundreds we have seen (Anderson 1994c) all carry the same kind of traces (Fig. 13). These blades often have thick deposits of bitumen (tar) adhering to them, preserving the imprint of the wood, in a few cases of insertion between logs. From 50 to 80 blades are mentioned in one text as making up the instrument, which corresponds well to the large size of the blades from the period having these traces. We have reconstructed this instrument (Anderson 1994c) and tested it over two seasons, and found its use does produce traces comparable to those on the blades from the Bronze Age. Flint inserts in modern sledges may become greatly rounded, unlike archaeological ones, because they contact the threshing floor directly at some points, or may be protected, today by wheels added to the sides of the plank which lift the blades up slightly off the threshing floor. Our reconstruction used wooden 'skis' to prevent blades from wearing too quickly on the threshing floor (Fig. 14).

Fig. 9. Underside of threshing sled from Turkey, showing cutting edges of flint (Fig. 8) inserted in grooves in the two assembled planks.

Fig. 10. Example of use of the threshing sled or tribulum in Turkey. Note weighting of board, pulled by oxen in a circular motion over cereals spread on a clay threshing floor, to chop straw and thresh grain.

Fig. 11. Reconstruction of threshing sled used in the Bronze Age, from descriptions in cuneiform texts. Small logs are lashed together with leather straps and blades (50) are set between the logs in rows, and fixed using a mixture of bitumen and fine sand. 'Skis' were added to create a small gap between the blade edges and threshing floor, both allowing efficient evacuation of chopped straw and threshed grain from under the sled, and reducing wear formation on blade edges.

Fig. 12. Both sides of a Canaanean blade fragmented and used in a Bronze Age threshing sled, according to use-traces (Fig. 13). Note gloss and bitumen traces corresponding to the set of the blade in the instrument. Wear on the edge is slightly toothed.

Fig. 13. Use-traces on the edge of a blade section like that in Fig. 12. Traces are like those in Fig. 8, with depressions including comet-shapes traces (arrows). Smooth bright areas show greater contact with plant material than with the threshing floor, corresponding to the results of the experiments (Figs. 11, 14).

Fig. 14. Experimentally made Bronze Age threshing sled being pulled over clay threshing floor covered with sheaves of bread wheat. Only stones were needed to weigh down this relatively small instrument for efficient chopping and threshing of the plant material. The photograph in the last column in Table 1 shows chopped straw on threshing floor after this experiment.

Fig. 15. Fragment of mud brick from a Neolithic site with domestic agriculture, showing imprints (arrow) of finely chopped straw used to temper the clay. This straw was probably chopped using an early form of threshing sled, then winnowed. Blades with wear similar to those in the experiment are found in the site.

Fig. 16. Silica phytolith from a cereal glume, magnified 400X, from an ashy deposit of chopped cereal straw and chaff, found in a building structure in a late Neolithic site in North Euphrates, Syria. Note sharp cut (arrow) of the silica sheet of phytoliths, very common in this deposit, which is neither a natural break nor the usual way these phytolith sheets break up in the soil. This cut corresponds probably to cutting with a blade set in a threshing instrument. Phytoliths cut in this way have been found in deposits on threshing floors after use of the tribulum, and the frequence of this observation at the site suggests this deposit represents plant material chopped using some early form of threshing sled (see Fig. 14).

We found that a quantity of sheaves harvested in 30 hours with a sickle, stacked on the threshing floor, was threshed and chopped by this relatively small instrument in only 3 hours! The product (figure in last column of Table 1) not only shows perfect threshing of the grain, but also corresponds to sizes of chopped straw we have seen used to temper mud brick constructions from archaeological sites. Table 1 shows that none of the stone tools examined from sites from the Bronze Age (5th millenium BP) carries traces indicating use for harvesting. Harvesting may have been accomplished using metal sickles, relatively rare objects at the time, which texts show were stored in central areas or melted down, so we would not expect to find them left on site from one season to

the next (J.-P. Grégoire, pers. comm.). Alternately, plants were pulled up without using tools, a harvesting technique that we found presented difficulties for threshing and winnowing, but which may be suggested by presence of culm bases among the archaeobotanical remains in one instance (J. McCorriston, pers. comm.).

A Neolithic instrument?

Cereal glumes, not chopped stems, tend to be used as tempering material for clay from structures in sites with wild cereal grain, and in these sites we do not find any tools with traces showing use for chopping of stems. This situation changes for sites with domestic cereals, where temper tends to be of chopped cereal stem fragments, and blades with traces from a tool like a threshing sledge begin to be identified (Table 1). These imprints in mud brick (Fig. 15) sometimes correspond to use of a size fraction of chopped straw which has been sorted (e.g. through winnowing), much as today for the straw threshed mechanically in Syria, where a particular size fraction is used to temper mud brick and other sizes are used for fuel and animal food. Another indication of the use of such an instrument at this time is provided by our analysis of a 1-m^2, 20-cm thick deposit, found in the corner of a late Neolithic structure from the site Halula in the Upper Euphrates (Anderson, unpublished). The deposit was made up of cereal phytoliths, not grains, representing burnt pieces of stem and glumes, cut (Fig. 16) in a manner characteristic of processing with the threshing sledge, according to analyses of material left on threshing floors after use of a threshing sled in the traditional way (Juan-Tresserras 1997) and our experiments described above (Fig. 14). The deposit, overlain by woven stem material, may correspond to a pillow or mattress and its stuffing, or to an area where chopped fragments were stored (in a bag?) for future use.

Indeed, a variety of uses of plant material processed by the tribulum is attested or likely, but it is not known whether this new tool was initially conceived to process increased amounts of grain, for human and animal consumption, or (also) to deal with a need for massive quantities of chopped stems (for architecture of greatly expanded habitation sites, but also as fodder, bedding, etc.). This instrument is pulled by animals traditionally, and the earliest traces of blades which could have armed it, from the late Neolithic, coincide with the earliest domestication of oxen (Anderson 1994c; Anderson and Inizan 1994; D. Helmer, pers. comm.).

Conclusions

Present data do not point to the existence of a universal 'wild plant food production phase' at this time, where humans would have regularly used all the basic agricultural techniques (of tilling, sowing, harvest, re-tilling and sowing) comprising agriculture of morphologically domesticated crops, to exploit morphologically wild cereals. This should not have the negative connotation of pushing the date for the beginning of agriculture ahead, but rather highlight the fact that Neolithic peoples were evidently adapting to and effectively exploiting cereal resources. On the other hand, once domestic agriculture began, new tools for threshing apparently came into use, resembling the traditional threshing sledge or tribulum. They correspond to a great increase in scale, both in quantity of cereal products produced and used, and in the complexity of the sequence of treatment of cereals. These data also serve to underline the ancient origins of the traditional threshing sledge. Appearance of the Neolithic agricultural assemblage in the Middle East is shown using criteria in Table 1, and its travel or diffusion may be mapped using locations where this instrument is attested [blades (Skakun 1992, 1993), remains of plants chopped with it, mud brick imprints, phytolith data, etc.] as well as clearly identified sickle blades, groundstone tools and cereal grain.

Acknowledgments

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Problems in Correlating Pollen Diagrams of the Near East: A Preliminary Report - R.T.J. Cappers, S. Bottema and H. Woldring

Introduction

Studies dealing with the transition from hunting/gathering to farming in the Near East focus on different aspects of this process. The main questions, which are closely related to each other, are why and how this transition took place.

An important contribution to the discussions dealing with these two questions comes from the study of pollen, which can be used for the reconstruction of past vegetation and climatic changes. To gain insight in these environmental aspects, many core samples from the Near East have been investigated during the last decades (Van Zeist and Bottema 1991; Bottema 1993).

The interpretation of pollen diagrams may be seriously hampered by problems in dating, which in turn may have consequences for both the correlation of pollen diagrams with each other (Rossignol-Strick 1995) and with the correlation of diagrams with occupation periods of archaeological sites.

Usually, the interpretation of radiocarbon dates of organic material from archaeological contexts does not give serious difficulties. The reason is that those dates are based on the measurements of ^{14}C that has been incorporated by organisms from the atmosphere. It is even possible to correct for fluctuations of the concentration of ^{14}C over considerable periods by calibration.

Dating of pollen diagrams, on the other hand, is more problematic. First, it is not always possible to obtain a reasonable number of dates from a single core because of insufficient amounts of organic material. This is especially true for the Near East, where most of the sediments consist of clay and, moreover, the organic fractions originate predominantly from the local vegetation. A related problem is that carbon may be incorporated by organisms originating from older sediments.

The concentration of ^{13}C differs in the various parts of the biosphere. This is partly the result of the differential uptake by plants. Organisms discriminate in the uptake of carbon isotopes, with a tendency for the lightest isotope. Thus ^{12}C will be taken up in preference to ^{13}C, and ^{13}C in preference to ^{14}C. This differential uptake is

referred to as fractionation and a correction for this process is a standard procedure in calculating the radiocarbon dates. A further correction, however, is possible by taking into account the variation in ^{13}C of different plant types (e.g. submerged and emerged water plants) in which ^{14}C activity can differ from 100% modern carbon (pMC).

Unlike ^{14}C, ^{13}C is a stable isotope, which makes it possible to measure its concentration irrespective of the age of the sediment. The concentration of ^{13}C is expressed as δ^{13}C, being the ^{13}C/^{12}C ratio in the sample relative to a standard (Mook 1987).

Another process which can make radiocarbon dates too old is contamination with older carbon-containing material. A correction is possible with the extrapolation method. This method is only applicable if a reasonable number of radiocarbon dates are available, a constant sedimentation rate can be assumed and no sediment is missing.

The correlation of pollen diagrams is hampered not only by problems in dating, but also by the complexity of the data matrices themselves. Pollen diagrams of the Near East represent altogether more than 500 different taxa. Of course, only a part of these taxa are present in a particular diagram. Still, the large number of taxa in a data matrix and the relatively large number of taxa with low counts make it difficult to incorporate all data in a pollen diagram. As a result, taxa which may be of importance because of their ecological information, and the appearance or disappearance of taxa with low percentages, may be poorly represented.

Correspondence analysis (CA) can be used to reduce the complexity of a data set. Carrying out this analysis on pollen data makes it easier to compare fluctuations in the composition of the spectra. Moreover, it is possible to arrange the taxa in a pollen diagram so that the vegetation history can be better visualized (Turner 1986; Birks 1993).

This article presents preliminary results dealing with the correlation of the pollen diagrams of Hula, Ghab and Eski Acigöl (Fig. 1). The analysis is limited to a selection of taxa, in which special emphasis is laid on the tree pollen. The pollen diagrams of Hula and Ghab have been published and discussed by Niklewski and van Zeist (1970), van Zeist and Woldring (1980) and Baruch and Bottema (1991). The publication of the pollen diagram of Eski Acigöl is in preparation (Woldring and Bottema) and the publication of the complete Hula diagram is in press (Baruch and Bottema 1998).

Material and methods

Correspondence analysis

Applied to pollen diagrams, correspondence analysis (CA) assumes a unidimensional model for describing the frequency distribution of each taxon as a function of depth. This relationship between frequency distributions of taxa and depth is assumed to be unimodal. Taxa may dominate at a specific depth, while their presence is decreasing in lower and upper parts of the diagram.

The CA was used to construct a tree curve for each of the pollen diagrams. This curve is based on the CA scores of the first axis. To facilitate the comparison between the three pollen diagrams, the curve for each diagram was calculated on the same scale. Thus, the data matrices were joined together for the analyses.

In first instance the complete pollen diagrams of Eski Acigöl (spectra 1-72), Ghab 1 (spectra 1-74) and Hula (spectra 1-138) were analyzed. Next, it was decided to exclude those parts of the pollen diagrams that were considered to be not relevant to the Pleistocene-Holocene transition. This reduction excluded the lower part of the Ghab 1 diagram (spectra 1-39) and the upper part of the Hula diagram (spectra 116-138).

A further reduction of the data set for this study concerned the exclusion of non-woody plants, with the exception of grasses (Gramineae), chenopods (Chenopodiaceae), mugworts (*Artemisia*) and members of the sedge family (Cyperaceae).

Fig. 1. Location of Eski Acigöl, Ghab and the Hula sites.
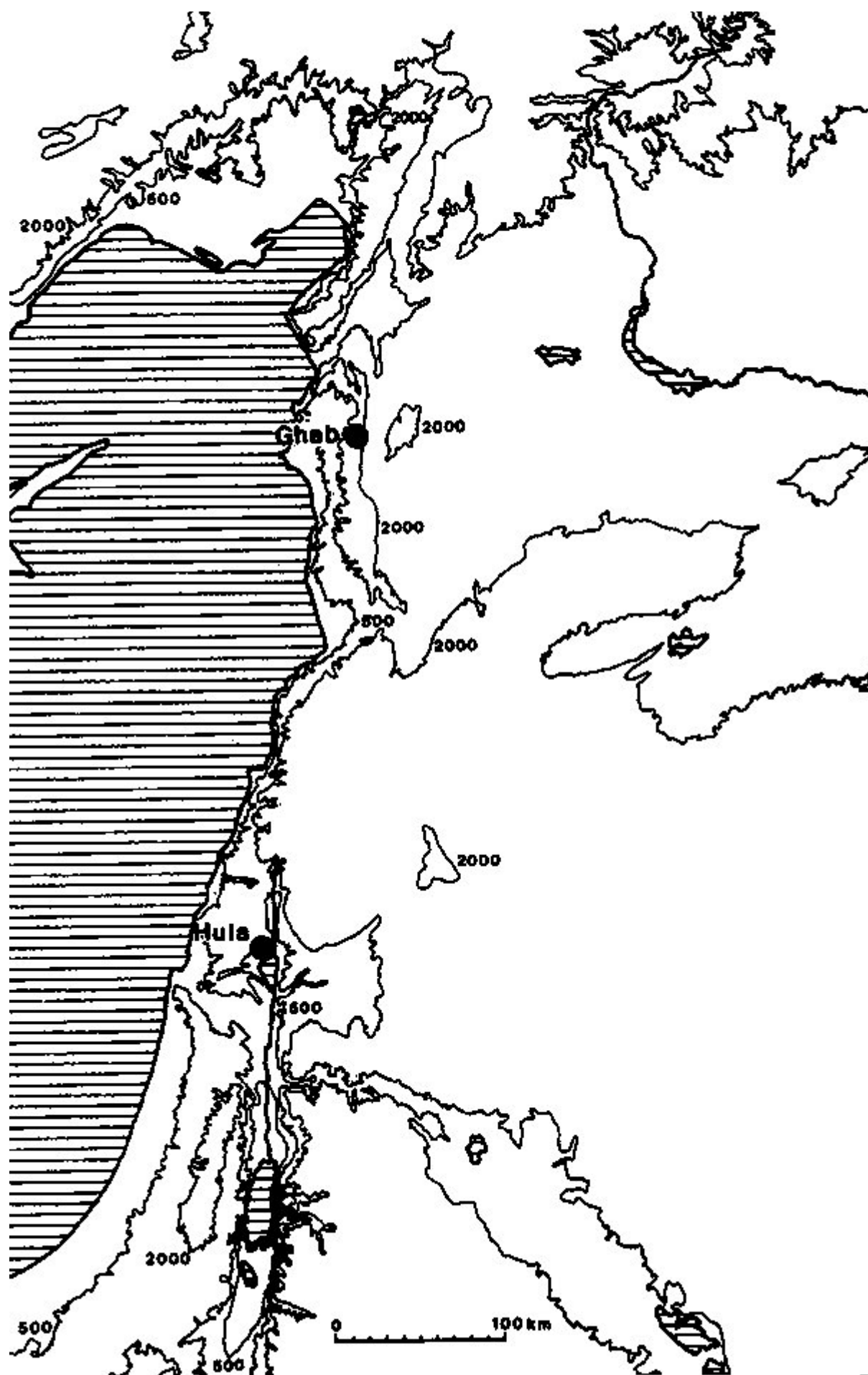
To investigate the influence of differences in dominance, analyses were carried out with both absolute counts and presence/absence scores. A further differentiation was made by analyzing both the complete data set of trees and a reduced data set in which only trees that are present in all three pollen diagrams were taken into account.

Some taxa were converted to other taxonomic levels, for example, *Quercus cerris*-type, *Q. robur*-type and *Q. ithaburensis*-type were considered as *Q. cerris*-type.

Corrections of radiocarbon dates

In addition to the standard correction of radiocarbon dates, a second correction was introduced which was calculated from:

$$t = -8033 \cdot \ln \frac{A_m}{A_c} \quad (\text{I})$$

where A_m is the measured ^{14}C activity and corresponds with the calculated BP value and A_c is the initial corrected activity and can be described by the equation:

$$A_c = X \cdot A_0 + (1 - X) \cdot 80 \quad (\text{II})$$

in which $A_0 = 100$ (related to emerged plants) and the assumed value of ^{14}C-% = 80 (related to submerged water plants), X is the contribution to emerged lake plants (assumed $\delta^{13}C = -16‰$) and (1 - X) is the contribution to submerged water plants (assumed $\delta^{13}C = -34‰$). Thus, the measured $\delta^{13}C$ can be expressed as:

$$\delta^{13}C = -34(1 - X) + -16(X) \quad (\text{III})$$

and X can be expressed as:

$$X = (\delta^{13}C + 34)/18 \quad (\text{IV})$$

The radiocarbon date of the core section 129-137 cm from the Ghab diagram (GrN 5810) was obtained from freshwater mollusc shells. Like water plants the molluscs may have incorporated fossil carbon. Therefore, a corrected date of 8580 BP is proposed, based on a reduction of the original activity to 85% (H.J. Streurman, pers. comm.).

With respect to the extrapolation method, a regression line was calculated through the original BP values. Extrapolated to the sediment surface, the intercept gives the deviation in relation to the original date. A correction is not applicable to dates from which the regression line has a negative intercept. This would indicate that the dates concerned are too young, which is not likely. Therefore, with respect to the Hula pollen diagram the extrapolation method was restricted to the five youngest radiocarbon dates (spectra 67-129).

Results

Information on the radiocarbon dates is summarized in Table 1. Because this overview is limited to the pollen spectra that were chosen for comparison, the two youngest dates of the Hula are not presented, although they were used for calculating the regression equation.

If an additional correction for $\delta^{13}C$ is applied, the radiocarbon dates of Hula are ca. 900 years too old and those of Acigöl ca. 1000 years. Using the extrapolation method, the corrections become even larger: the dates of the upper part of the Hula core are ca. 1350 years too old and all dates of Acigöl are ca. 3850 years too old.

Figure 2 presents a selection of the curves of the pollen diagrams of Hula, Ghab and Acigöl. The arboreal pollen (AP) curves in Fig. 2 show the fluctuations in the proportion of the tree pollen in comparison with the non-arboreal pollen which reflects the alternate expansion and reduction of forest and open vegetation.

The tree curves as calculated with correspondence analysis (CA curves) are shown in Figure 3. Contrary to the AP curves, they express both qualitative and quantitative information. A spectrum with an average composition of trees, as calculated from the data of all the spectra, has value 0 (e.g. solid line in spectrum 4 of the Hula diagram, Fig. 3). If all spectra had exactly the same tree pollen, that is not only the same pollen types but also the same number of pollen from each type, the curve would coincide with the vertical axis which is centralized on the X-axis. The more the composition of a certain spectrum deviates from the mean composition, the more it is projected to the left or to the right. The direction of the projection (i.e. a negative or positive score on the X-axis) has only a relative meaning. Because the data from Hula, Ghab and Acigöl were treated as one file, the scores

on the X-axes are comparable.

Table 1. Radiocarbon dates of Hula and Eski Acigöl. Radiocarbon dates are uncalibrated and presented without correction (1), with correction based on δ^{13}C (2) and with correction based on linear regression (3).

| Lab. no.	Lithology	Depth (cm)	δ^{13}C	Age BP (1)	Age BP (2)	Age BP (3)
Hula (spectra 1-115)						
GrN 22396	organic	315-325	-21.2	4140±50	3660	2790
GrN 22397	organic	595-605	-25.6	7000±70	6100	5650
GrN 22398	organic	823-834	-26.4	8670±120	7700	7320
GrN 17067	gyttja	995-1015	-27.3	9270±120	8200	-
GrN 17068	gyttja	1120-1140	-27.1	10,440±120	9400	-
GrN 14986	organic	1235-1242	-22.3	11,540±100	10,960	-
GrN 22399	organic	1475-1500	-26.9	15,580±220	14,540	-
GrN 14463	gyttja	1600-1625	-27.5	17,140±220	16,040	-
GrN 22402	carbonate	315-325	-2.4	39301±50		
GrN 22403	carbonate	595-605	-3.1	7020±60		
GrN 22404	carbonate	823-834	-2.3	12,130±90		
GrN 22405	carbonate	1475-1500	-4.2	18,950±200		
Eski Acigöl (spectra 1-72)						
GrN 21037	organic	262-264	-27.7	55401±280	4420	1690
GrN 22881	organic	455-460	-18.1	6610±60	6430	2760
GrN 21036	organic	663-665	-28.2	9440±230	8270	5590
GrN 22447	organic	832-836	-27.1	11,3601±100	10,300	7510
GrN 22605	organic	836-840	-25.2	10,910±100	10,040	7060
GrN 21035	organic	1044-1049	-28.9	11,590±180	10,350	7740
GrN 20633	gyttja	1161-1165	-29.1	13,450±150	12,200	9600
GrN 19988	organic	1450-1455	-30.7	14,320±170	12,890	10,470
GrN 22882	carbonate	455-465	13	6535±70		
GrN 22448	carbonate	836-840	10	11,960±260		
GrN 19989	carbonate	1450-1455	10	15,200±220		

Fig. 2. Selection of curves from pollen diagrams for the Hula, Ghab and Eski Acigöl sites. (AP = arboreal pollen, GRA = Gramineae, CHE = Chenopodiaceae, ART = *Artemisia,* CYP = Cyperaceae, CER = Cerealia, CHE/ATR = Chenopodiaceae and *Atriplex*).
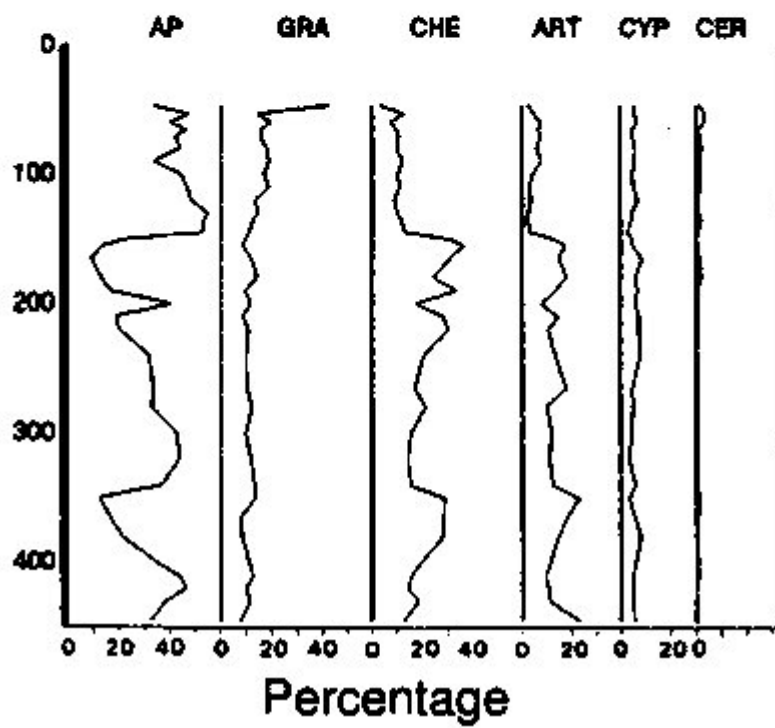
Percentage

Acikgol


Percentage

Ghab

Percentage
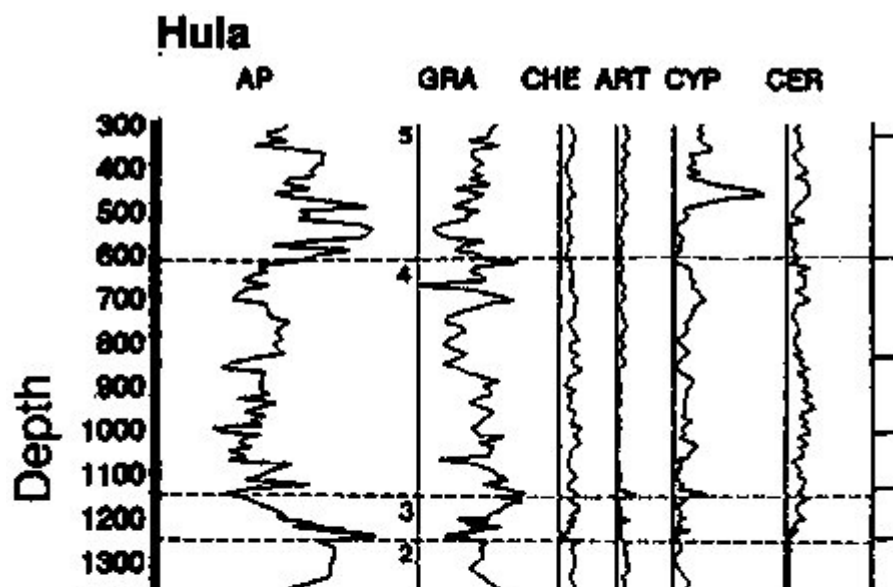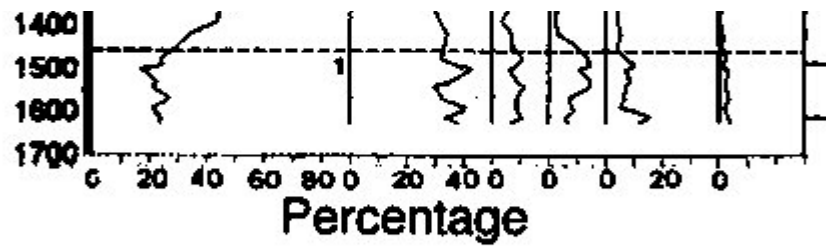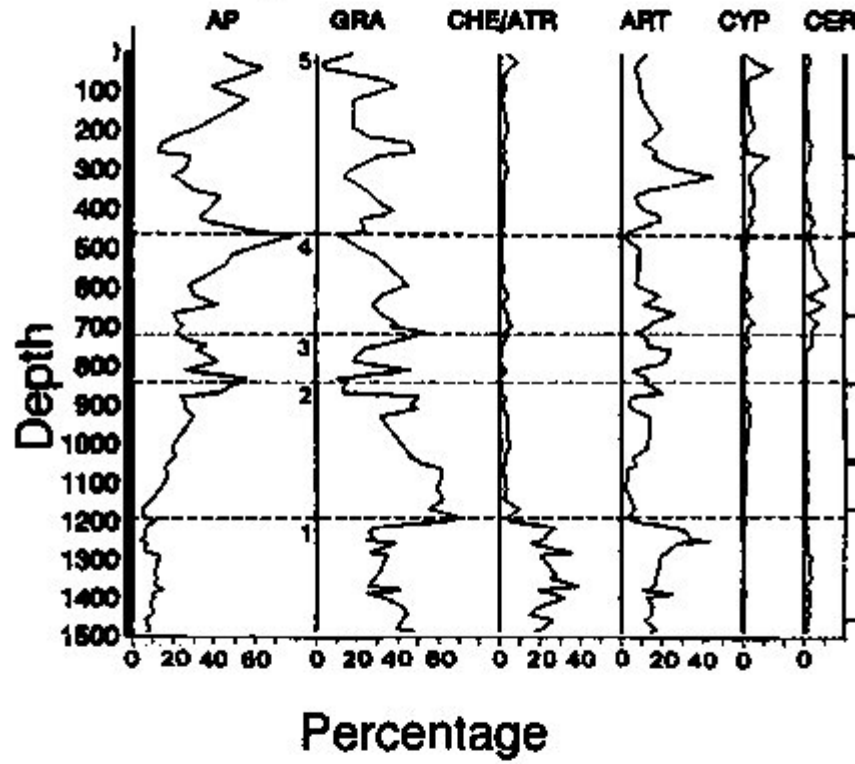
From the four curves that have been calculated using correspondence analyses, only two are presented for each

pollen diagram (Fig. 3). The two curves based on presence/absence (dotted lines) fluctuate considerably, indicating that the composition of tree taxa is quite variable. It was therefore decided to present only the curve showing the fluctuation of the 27 taxa that are present in all three diagrams. This curve represents 61% of the total number of trees in Hula, 55% of the trees in Acigöl and 71% of the trees in Ghab. A less fluctuating pattern is shown by the two curves based on the occurrences (straight lines).

Fig. 3. Tree curves calculated with correspondence analysis for the Hula, Ghab and Eski Acigöl sites.

Ghab

1st CA-axis

10,080±65 BP

1st CA-axis
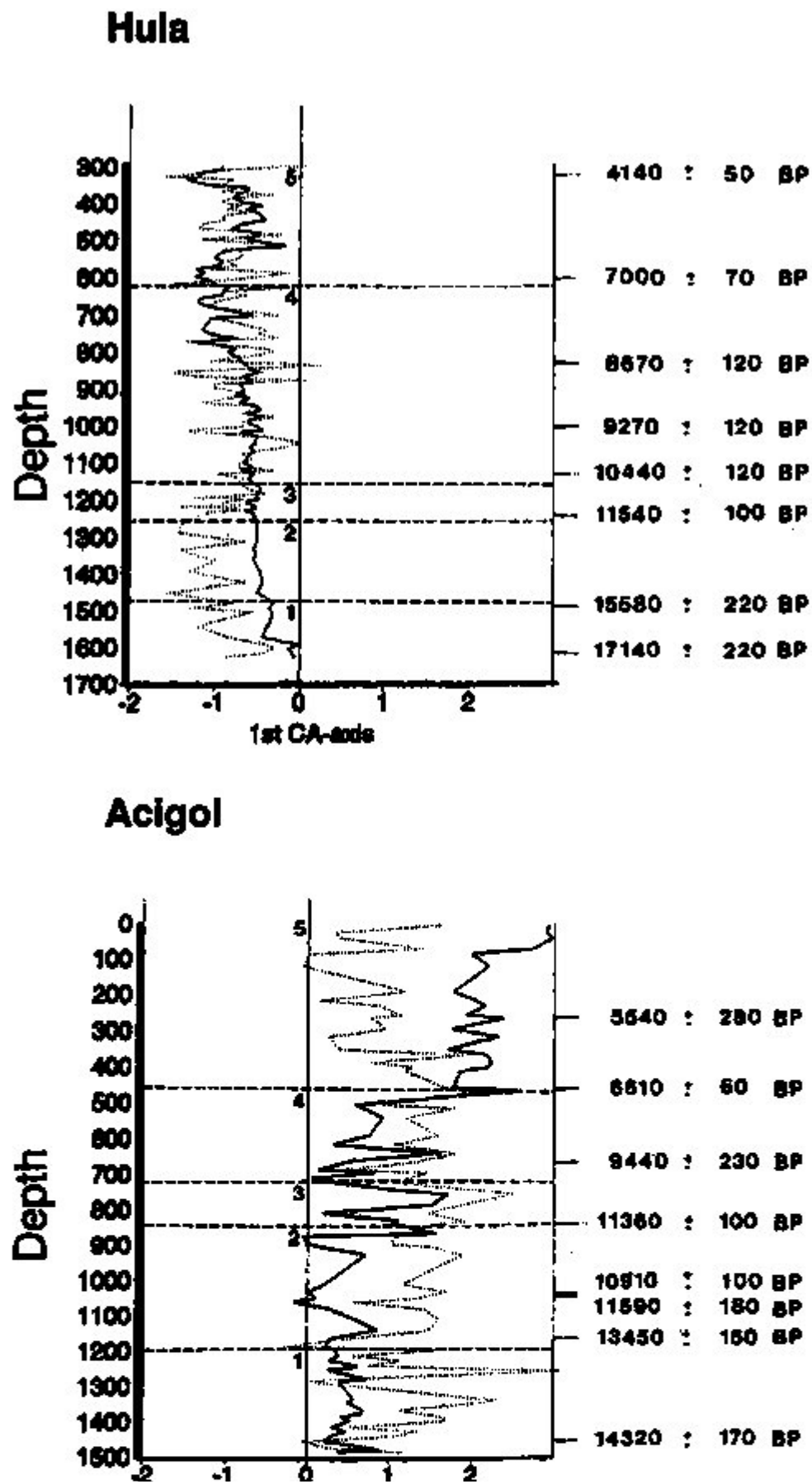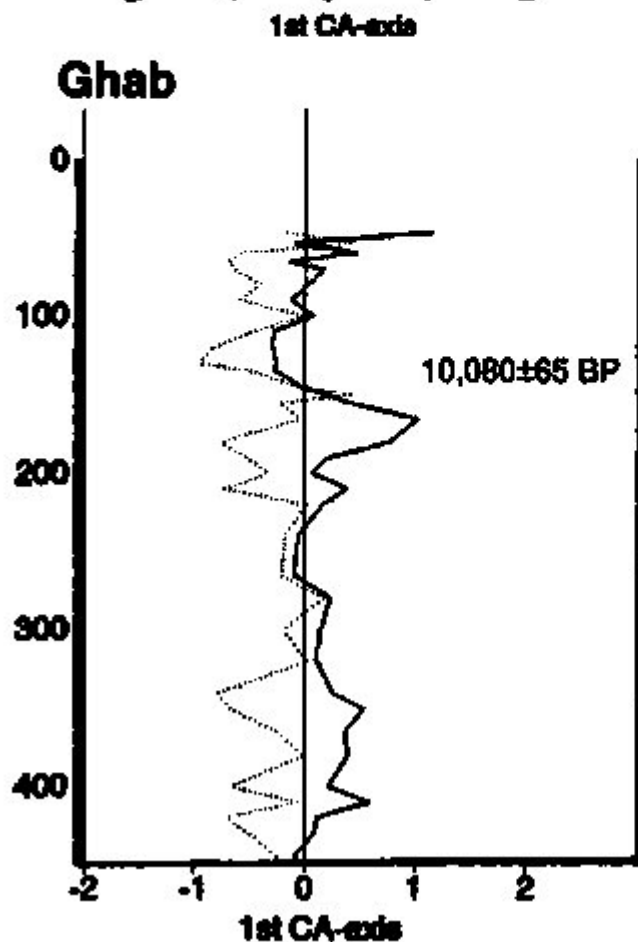
The Ghab diagram takes an intermediate position in terms of the tree pollen composition of the spectra (Fig. 3). Only in the lower part of their diagrams do both Hula and Acigöl resemble the composition of the Ghab diagram to some extent. In the middle and upper part, however, the curves of Hula and Acigöl increasingly diverge from the Ghab curve in an opposite direction, indicating that in both areas a different combination of tree taxa becomes dominant, which can be explained by differences in latitude and altitude.

The pollen diagrams of Hula and Acigöl have been subdivided into five zones based on the curves in Figures 2 and 3, showing a similar pattern in the vegetation development. A short characterization will be given below of each of these zones. The correlation with the Ghab diagram will be discussed in the next section.

Zone 1 is characterized by relatively low tree pollen percentages. Gramineae, Chenopodiaceae, *Artemisia* and Cyperaceae, on the other hand, have fairly high pollen percentages.

Zone 2 is characterized by increasing AP values to a maximum of 76% in Hula and 56% in Acigöl. In both diagrams *Quercus cerris*-type is the predominating tree, in which probably Q. *ithaburensis* accounts for most of the deciduous oak pollen in Hula and probably Q. *pubescens* and/or *robur* for those of Acigöl. The increasing values of both *Pinus* and *Juniperus* in the second part of this zone in the Acigöl diagram are responsible for the strong fluctuation of the CA curve (Fig. 3). The relatively high percentages of Chenopodiaceae, *Artemisia* and Cyperaceae drop quickly to low values at Hula and Acigöl (Fig. 2). In Acigöl, where these herbs were represented by higher values, this decrease is compensated by the Gramineae, although trees expand at the expense of grasses toward the end of zone 2.

A decline of tree pollen percentages is shown in zone 3, mainly compensated by Gramineae and in Acigöl also by *Artemisia.* Again the composition of the tree assemblage is more variable in Acigöl than in the Hula (Fig. 3). Especially *Corylus* and *Cedrus* increase in pollen percentages, a process initiated even before the transition to the third zone. In both Hula and Acigöl the percentage of Cerealia pollen increases.

In zone 4 the percentages of the tree pollen increase again. In the Hula Q. *ithaburensis*-type*, Q. calliprinos*-type and *Olea* are dominant. The considerable increase of the last one from the upper half of this zone onwards is responsible for the shift in the CA curve (Fig. 3). In Acigöl this zone is dominated by Q. *robur*-type, *Pinus* and *Cedrus.*

The last zone starts with an increase of the tree pollen percentages in the Hula and with a decrease of those in

Acigöl. The CA curve of Acigöl shows that despite fluctuations in tree pollen percentages the composition has been strongly changed. This can be attributed mainly to the increase of *Pinus* at the expense of *Q. robur*-type. *Pinus* also becomes one of the dominant trees in the Hula, though its percentages remain considerable lower than that of *Q. ithaburensis*-type, *Q. calliprinos*-type and *Olea*.

Discussion

On the basis of radiocarbon dates that have been corrected by the $\delta^{13}C$ values, the increase of the tree pollen in the Hula diagram can be dated at ca. 14,500 BP (boundary zone 1-2). This increase continues until ca. 11,000 BP, after which the tree pollen starts to decrease until ca. 9500 BP (zone 3). This climatic deterioration could be coupled with the Younger Dryas, though it has to be stressed that this period is less recognizable in pollen diagrams from the Near East than in diagrams of Europe (Bottema 1995). From ca. 9500 to 6100 BP (zone 4) the tree pollen percentages increase only gradually and from ca. 6100 BP onward (zone 5) this increase is more substantial. Taking into account a correction on the basis of the extrapolation method, the gradual increase in zone 4 could have lasted several hundred years longer (Table 2).

This pattern of increase and decrease of tree pollen percentages is also represented in the Acigöl diagram, although the zones distinguished are dated much younger. The boundary between zones 1 and 2 (first increase of tree pollen) is dated ca. 2100-2300 radiocarbon years later. Taking into account the extrapolation method, the discrepancy between Hula and Acigöl is ca. 4900 radiocarbon years for this boundary. And even if the uncorrected dates of Acigöl are compared with the corrected ones of the Hula, there is still a difference of ca. 1000 radiocarbon years.

Table 2. Radiocarbon dates of the boundaries of the five zones that are distinguished in the pollen diagrams of Hula and Eski Acigöl. The standard dates have been corrected on the basis of $\delta^{13}C$ and the extrapolation method.

	BP (standard)	BP ($\delta^{13}C$ corrected)	BP (extrapolated)
Hula			
Boundary 4-5	7000	6100	5650
Boundary 3-4	10,600	9500	9500
Boundary 2-3	11,540	10,960	10,960
Boundary 1 -2	15,580	14,540	14,540
Eski Acigöl			
Boundary 4-5	6600	6400	2750
Boundary 3-4	10,000	8400	6000
Boundary 2-3	11,360	10,300	7500
Boundary 1 -2	13,450	12,200	9600

Whereas the extrapolation method is responsible for only relatively minor corrections of the radiocarbon dates of the Hula, it seriously affects those of Acigöl. A possible explanation for the larger corrections of the radiocarbon dates of Acigöl could be that, besides the uptake of old carbon by water plants, the sediments also became contaminated with older sediments. Eski Acigöl is a small, recently drained crater lake at the foot of the Karapinar volcano. The older sediments could have originated from the slopes of this volcano.

Another possibility is that volcanic activity was responsible for the age shift. Volcanic gases do contain carbon, but this is too old to be radioactive. Consequently it dilutes the concentration of the carbon isotopes in the surrounding air for which reason local plants are dated 1000 or more radiocarbon years too old. There is, however, scholarly disagreement on the effect of volcanic activity on radiocarbon dates. Despite older dates of recent plants near volcanos, radiocarbon dates for the eruption that destroyed Akrotiri (Santorini, Greece) are surprisingly close to dates given by other techniques (Bowman 1990).

It is also possible that in Eski Acigöl the upper part of the sediment is missing, resulting in a misinterpretation of the intercept. An indication for its absence could be the presence of strongly disintegrated peat at the edge of the drained lake, although this explanation seems not very likely. To make sure of this possibility, additional radiocarbon dates will be obtained from the upper sediment. Also the counting of varves can be used for an additional check on the radiocarbon dates.

The correlation of the Ghab diagram with that of the Hula and Acigöl is problematic because only one radiocarbon date is present in the part of the Ghab core that is under discussion. The dated sediment consists of

freshwater mollusc shells which makes an inaccurate dating very likely, as was mentioned before (Niklewski and van Zeist 1970). Without a correction for this radiocarbon date the pattern of the tree pollen curve is conflicting with that of the lower part of the Hula diagram. Using the corrected date of 8580 BP it is possible to coincide the tree pollen curve of Ghab with that of the Hula, especially if a slower sedimentation rate is taken into account for the lower part of the diagram, as was proposed by Hillman (1996). This lower part of the Ghab diagram remains problematic, however, with respect to the percentages of Gramineae, Chenopodiaceae and *Artemisia,* which have relatively high values comparable with zone 2 and 3 of the Hula diagram.

One radiocarbon date in the upper part of the Ghab diagram offers a high degree of freedom in correlating it with the well-dated Hula diagram. Using the corrected radiocarbon date, it is shown that a correlation is possible. The well-dated Acigöl diagram, on the other hand, demonstrates that a correlation based on the vegetation development can be problematic. A similar development is dated much younger in the Acigöl diagram, indicating that a shift in this development may have occurred in a south-north direction.

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Investigations of Botanical Remains from Nevali Çori PPNB, Turkey: A Short Interim Report - R. Pasternak

The site

Nevali Çori (NÇ) is located near the Turkish town of Urfa (37°60'N, 38°70'E, 490 m above sea level) on the slope of a Euphrates side valley. The ^{14}C analyses, only available from the early levels, provided dates of ca. 8400 BC (calibrated). The settlement was occupied from the Early PPNB to the early Bronze Age (Hauptmann 1984, 1987, 1988, 1997). The PPNB layers included stone houses and a temple building of around 200 m[2]. On the slope in front of the houses a 'roasting-pit area' was found with a number of hearths in close proximity to each other. Most of these hearths were in use during the earliest phases.

Samples, methods and results

In 1991, 267 samples were taken, with a hand sieve of 0.35 mm, from the PPNB layers. The average sample volume was 10 liters. One-half of the samples were taken from areas on the site that appeared to have good potential for archaeobotanical results. These were essentially areas associated with hearths. The hearths themselves contained only a small number of poorly preserved plant remains. The other half were random samples collected from different parts of the excavation. The material used to fill the space between the stones of the big temple wall contained a lot of charred botanical remains. The composition of remains in these samples was similar to those from the areas associated with the hearths. The results are presented in Table 1. This database is available from the author in electronic form.

Cereals

Triticum spp., wheats. There were 26,792 items identified as wheat. The wheats in all PPNB layers of NÇ are morphologically domestic. Nearly all spikelet forks show the typical tear-off points of non-brittle spikes.

Problems of determination

On the whole, hulled wheats have distinct phenotypic flexibility. Because the diploid *T. boeoticum* and the tetraploid *T. dicoccoides* both produce one - and two-seeded spikelets, the determination of a grain from a one - or two-seeded spikelet gives no information about the species and thus no information about the ploidy level. After extensive comparative research on modern grains and spikelet forks it was decided that, with the exception of the terminal spikelet forks, the ancient material gives no information about the species and the ploidy level.

From the ancient wheat grains, 661 one-seeded and 129 two-seeded grains were recorded. Only a small number of the grains are complete, so measurements were not possible. The approximate size is given in the drawings. There appear to be two different types of grains: small (Fig. 1) and large (Fig. 2). Most of the grains belong to the smaller type. Only 30 grains belong to the larger type. Four of these are obviously two-seeded and could be identified as *T. dicoccum,* the others as *T. monococcum.* But I decided that because of the overlap resulting from morphological variation the identification cannot be certain.

Table 1. The results of the analysis of 267 samples of PPNB layers of Nevali Çori (for the counts of finds fragments of seeds, fruits and shells were put together to a unit and then counted as one). All data are available as a dBase 3+ file.

Glume bases/spikelet forks/rachis fragments:	27,569
Seeds/fruits:	7342
Total:	34,911

Cereals

Triticum spp., one-seeded type	661
Triticum spp., two-seeded type	129
Spikelet forks of both types	26,002
Unidentified cereals	1067

Pulses

Lens	342
Pisum	137
Vicia ervilia	95
Lathyrus 'sativus'	137
Vicia faba	15
cf. *Cicer*	1

Unidentified pulses	1003
Fruits and nuts	
Pistacia, nut shells	470
Pistacia, complete	95
Amygdalus	29
Prunus spp.	19
Vitis	4
Cornus mas	1
Celtis	1
Grasses	
Hordeum distichon/spontaneum	89
Rachis fragments	1528
Bromus arvensis-type	27
Bromus, long-seeded	11
Lolium, small-seeded	4
Stipa spp.	1
Lolium cf. *temulentum*	1
Aegilops, glume-bases	27
Phragmites, fragment of culm	1
Unidentified Gramineae	194
Other plants	
Malva	1
Verbena officinalis	2
Fabaceae, *Trifolium*-type	3
Vicia-type	11
Polygonum persicaria-type	1
Galium, large-seeded	33
Galium, small-seeded	5
Bupleurum cf. *rotundifolium*	3
Glaucium corniculatum	18
Lithospermum cf. *tenuiflorum*	127
Solanum nigrum	1
Artemisia	210
Apiaceae cf. *Bupleurum*	2
Rumex spp.	2
Centaurea	2
Plantago	1
Portulaca oleracea	1
Papaver argemone-type	3
Asteraceae cf. *Achillea*	2
Ranunculus spp.	1
Helianthemum salicifolium	1275
Equisetum, Sporophyllae	2
Chenopodiaceae	73
Brassicaceae	508
Caryophyllaceae	11
Asteraceae	28
Lamiaceae	4
Polygonaceae	13
Solanaceae	2
Papaveraceae	11
Rubiaceae	1
Primulaceae	1

Cucurbitaceae	1
Boraginaceae	5
Unidentified seeds	360

Concerning the spikelet forks nearly 70% of the charred remains are spikelet forks of *Triticum.* They occur consistently in all layers. Around 60% of the spikelet forks are broken. Most of them are small. Around 500 complete spikelet forks were found in the fraction below 0.5 mm (Fig. 3). Twenty-three terminal spikelet forks were found and these indicate the presence of tetraploid wheats (Fig. 4).

Fig. 1. *Triticum* grains from NÇ, small-type. From the top: first is probably two-seeded, second is two-seeded, third and fourth one-seeded, and fifth probably one-seeded.
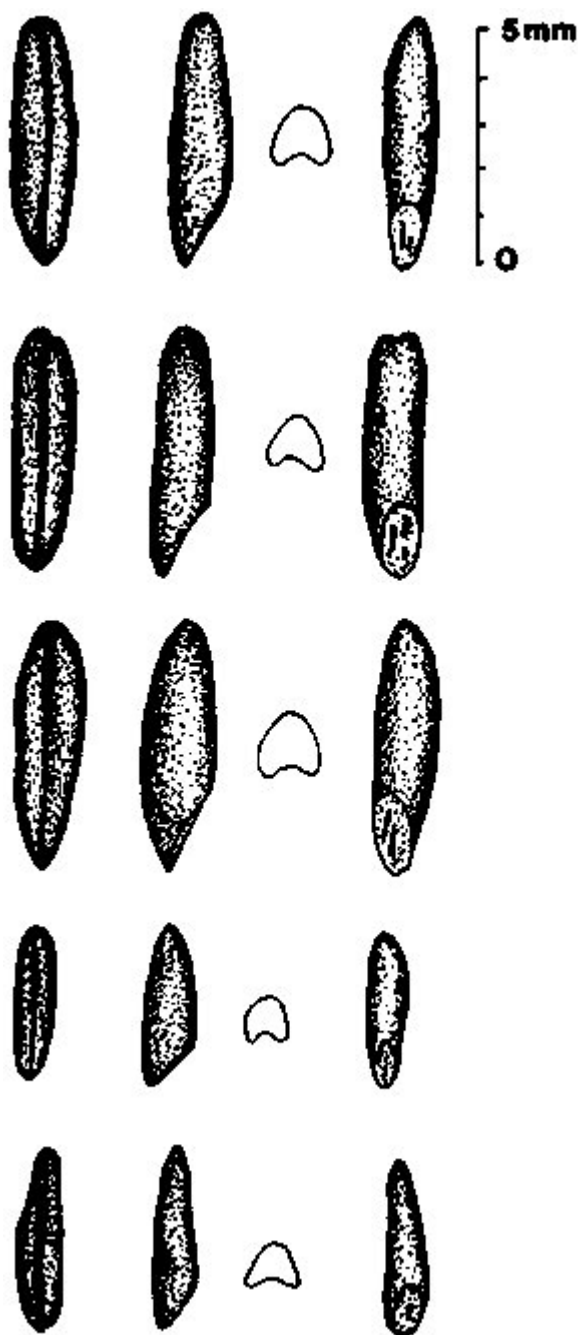

Fig. 2. *Triticum* grain from NÇ, large-type. From the top: the first one is a complete grain, second, third and fourth are typical broken grains.
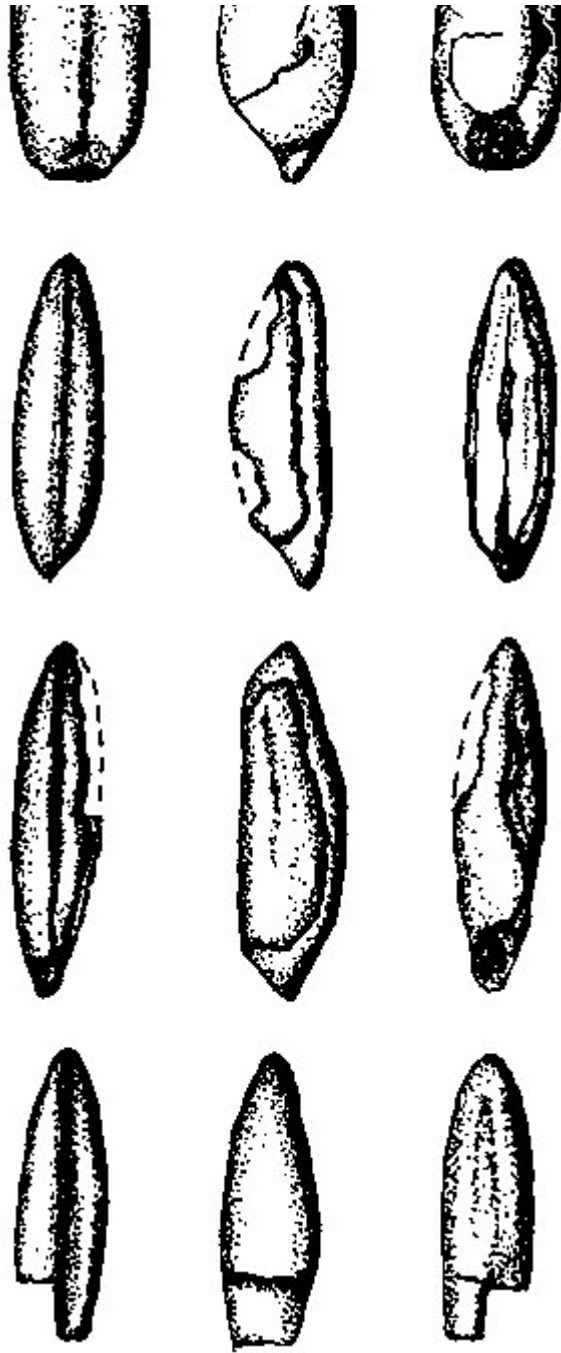
Fig. 3. *Triticum* spikelet forks from NÇ with the typical tear-off markings of non-brittle spikes.

Fig. 4. Terminal spikelet forks of *Triticum* from NÇ.
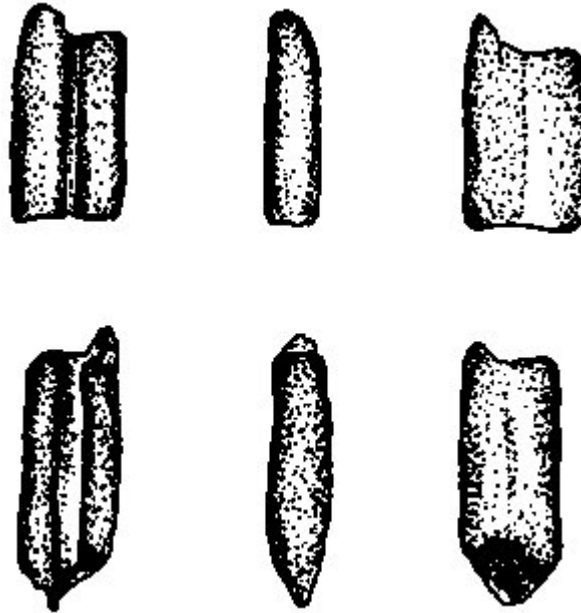
Fig. 5. Fragments of *Hordeum* spp. from NÇ.

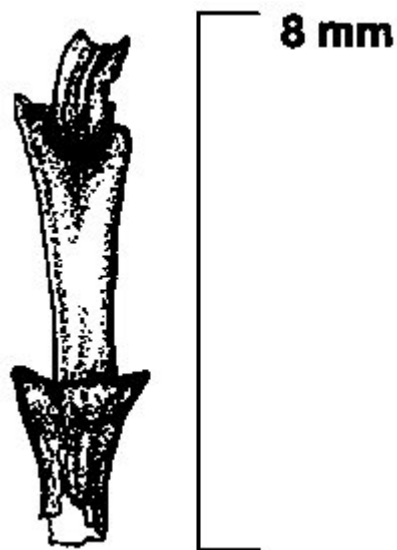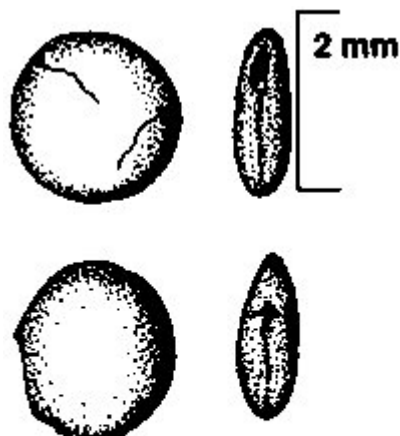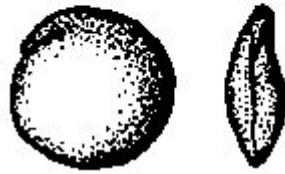**Fig. 6. Well-preserved rachis fragments of *Hordeum* from NÇ (probably *Hordeum spontaneum*).**

8 mm

Fig. 7. Typical seeds of *Lens* from NÇ.

2 mm

Approximately 89 broken grains of *Hordeum,* barley, were recovered. They were small and slender with distinct edges (Fig. 5). It was not possible to make a distinction between *Hordeum distichon* and *H. spontaneum.* More than 1500 rachis fragments were found occurring in all layers. With a small number of exceptions they are very small; one-third was found in the fraction below 0.5 mm. Most of them are small, badly preserved fragments. In comparison with those of Çayönü (van Zeist and de Roller 1991/1992), the poorly preserved fragments were identified as *Hordeum* subsp. The well-preserved rachis fragments appear to belong to *H. spontaneum* (Fig. 6). Whether they are cultivated or wild is difficult to ascertain.

Pulses

The number of pulses, totalling 1726 seeds, is nearly as great as the number of cereal grains, which totalled 1946. This clearly shows the importance of vegetable protein during this period. At least five species were present in the PPNB layers.

***Lens* spp.:** Lentil is the most frequent species. Most of the 342 seeds of NÇ are very small. Only one reached a diameter of 3 mm; the average diameter of all the others is about 2.2 mm with an average thickness about 1.2 mm (Fig. 7).

***Pisum* spp.:** 137 seeds of pea provide evidence for the use of this pulse during Early PPNB. About a dozen seeds show typical traces of shrinking, probably from drying prior to charring (Fig. 8). The average diameter of the seeds is around 4.5 mm. Most of the peas were found in low frequencies associated with hearths in the 'roasting-pit-area'. Hence they may represent seeds lost during cooking.

***Lathyrus* subsp., cultivated grass pea:** The 137 seed remains show the similar importance of grass pea as compared with pea. Seeds showing a hatchet-like lateral view predominate (Fig. 9). The grass pea seeds show several morphological types. Hence a definite identification as *Lathyrus sativus* is not possible.

Another small-seeded pulse with a diameter of 3 mm was found. It closely resembles *Cicer* or *Lathyrus cicera.* Since this single seed is poorly preserved, no precise identification was possible.

***Vicia ervilia,* bitter vetch:** Despite the small size of the seeds and the possible toxicity, bitter vetch was obviously in use. Nearly 100 seeds were found and probably a lot of the small unidentified pulses were also bitter vetch (Fig. 10). Bitter vetch is a small plant without tendrils. In the field it is difficult to eliminate when it grows with lentils. The plant tolerates very dry conditions and has a short vegetative period of 120 days.

***Vicia faba,* horse bean:** Only 15 poorly preserved seeds of horse bean were found (Fig. 11). Most of them are broken.

Fruits and nuts

***Pistacia* spp., terebinth:** *Pistacia* nuts were frequently consumed. Of the 470 nutshells found, most were broken, only a few of them completely preserved. *Pistacia* is often found on Neolithic sites in the Near East. The botanical remains from NÇ show that these nutrient nuts were roasted. Numerous blistered-charred fragments were found. Roasting reduces the bitter aspects in taste and changes the carbohydrates partially into sugar. This is evidence for food-processing, rarely found in archaebotanical remains.

***Amygdalus* spp., almond:** Almonds were probably eaten during the Neolithic NÇ. Fragments of nutshells (Fig. 12), together around 30 nuts, were found near the hearths. In small amounts almonds are not poisonous for adults. The kernels contain cyanogene glycosides that break down to hydrocyanic acid, up to 1 mg per nut. *Prunus dulcis* var. *dulcis* is poor in these substances and can be consumed in greater quantity. The fragments found do not allow identification of the species, so it is not known if the almonds of NÇ were toxic or not.

***Vitis* spp., grape:** Two of the four grape pips are completely preserved (Fig. 13). The pips indicate that the fruit was small, probably gathered early in the unripe state, before birds or other animals ate them. The wild grape vines probably grew in the Euphrates Valley.

Fig. 8. Three different seeds of *Pisum* from NÇ. The bottom sample is a small seed of *Pisum* showing

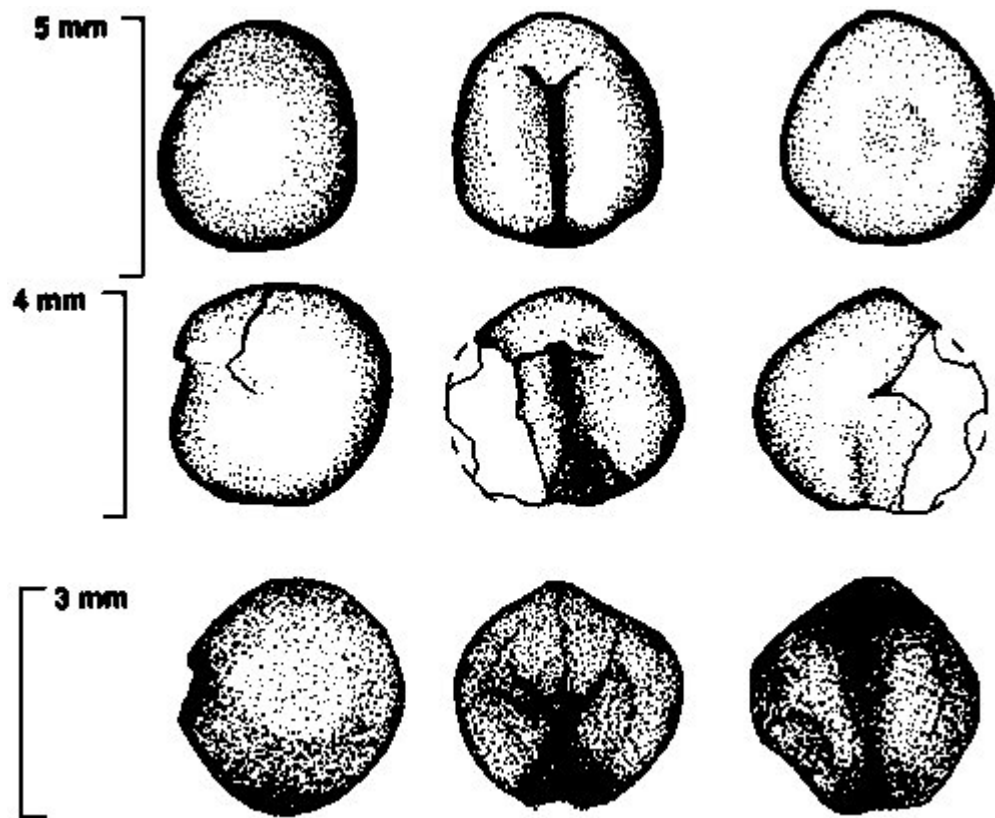**depressions, probably due to drying.**

5 mm

4 mm

3 mm

Fig. 9. *Lathyrus 'sativus'* from NÇ. The top first and second are seeds with hatchet-like shape from the proximal part of the pod. The bottom one is seed from the middle of a pod.
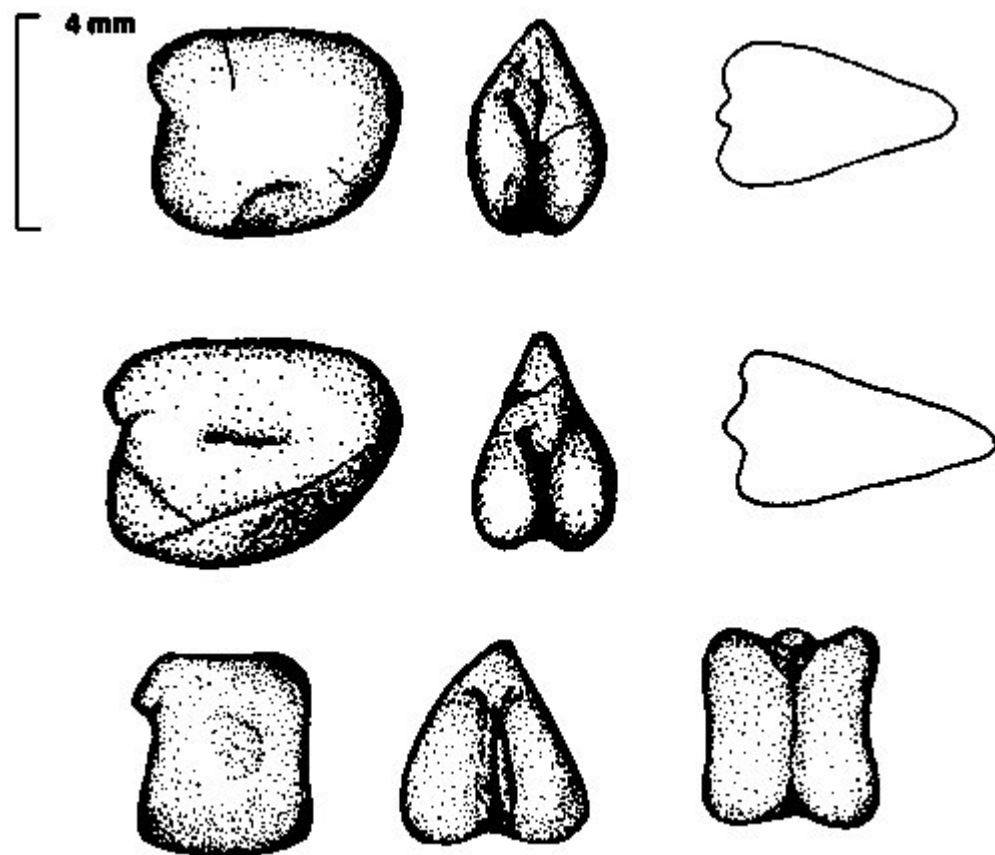
4 mm

Fig. 10. *Vicia ervilia* from NÇ.

2 mm

Fig. 11. *Vicia faba* from NÇ.

Fig. 12. *Amygdalus* stone from NÇ.

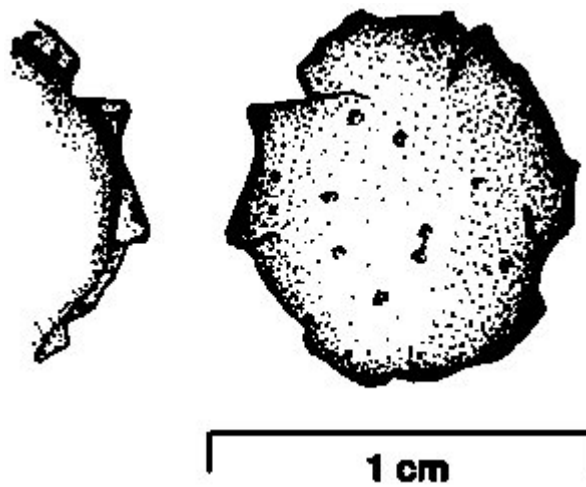

1 cm

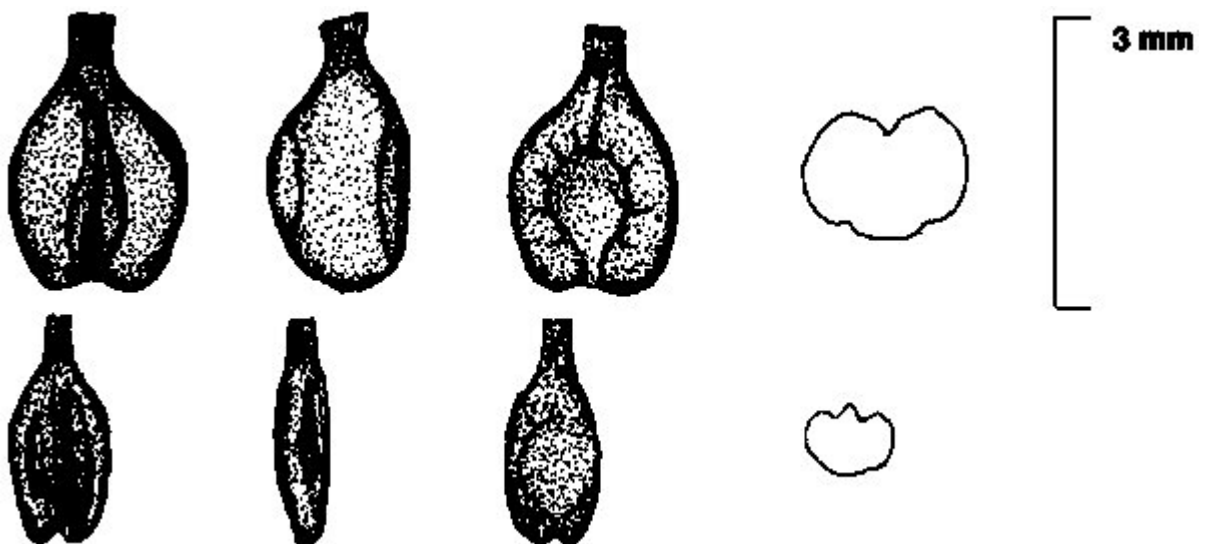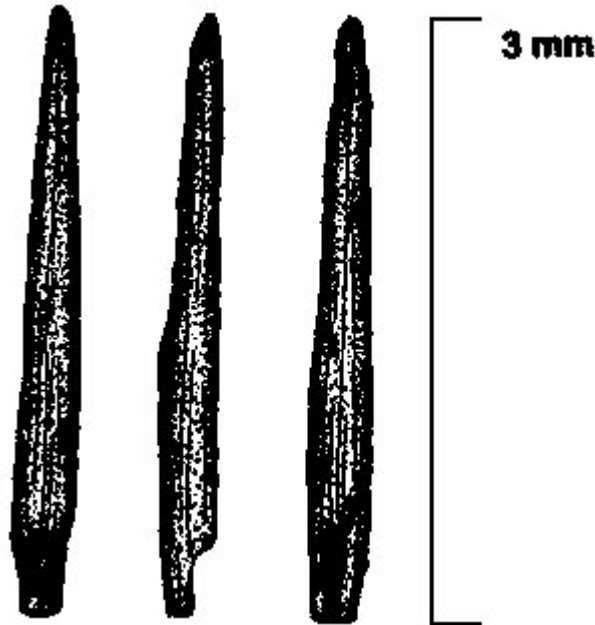**Fig. 13.** *Vitis* seeds from NÇ.

3 mm

Fig. 14. *Celtis* stone from NÇ.

7 mm

Fig. 15. *Stipa* from NÇ.

Cornus mas, Celtis australis, Prunus spp.: Only one item of each of these was recorded. The seed of *Celtis* is mineralized (Fig. 14). *Cornus* and *Celtis* might have been used not only as fruits, but could have been helpful as medicinal plants as well. The remains of these two species and those of *Prunus* complete a picture of a distinct diversity of plants in use at this site.

Other seeds

More than 300 seeds of Gramineae were found representing at least 10 different species. *Bromus* and seeds resembling *Alopecurus* were the most numerous. The presence of *Aegilops* is recorded by 27 glume bases. Five seeds of *Lolium* indicate an early association of this species with cereal cultivation. Surprisingly a very brittle grain of *Stipa* (Fig. 15) was completely preserved.

Nearly 1275 remains of *Helianthemum salicifolium* and 210 remains of *Artemisia* species indicate dry conditions.

Conclusion

The plant remains of NÇ. represent early evidence of food production. Wheats and diverse species of pulses were cultivated. The work on modern material casts doubt as to whether the two-seeded wheats found on Neolithic sites of the Near East are tetraploid or diploid. The only conclusive proof we have is terminal spikelet forks which record the existence of tetraploid wheats in the material. A wide diversity of different wheats appears to have been in use during the early Neolithic. We still do not know how long the domestication process took.

Probably the botanical remains from the Early PPNB layers of NC do not represent the very beginning of food production. Given the advanced architecture, even in the earliest levels, it is not improbable that food production dates from before the occupation of the site and was introduced from elsewhere.

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Crop Water Availability from a Pre-Pottery Neolithic Site on the Euphrates, Determined by Carbon Isotope Discrimination of Seeds - J.L. Araus, A. Febrero, M. Catalá, M. Molist, I. Romagosa and J. Voltas

Introduction

The beginnings of agriculture in the Old World, which occurred sometime during the period of transition from hunting/gathering to farming communities, seem to be associated with cereal domestication. Indeed, experimental studies have given a theoretical indication of a lapse in time between the beginnings of cultivation and morphological domestication (Hillman and Davies 1990; Willcox 1991, 1992), but up to now cultivation prior to morphological domestication has not been identified from plant remains in the Near East (Willcox 1996). The Pre-Pottery (aceramic) Neolithic site of Tell Halula is the oldest reported archaeological site on the Euphrates where domesticated crops have been reported (Molist *et al.* 1995; Willcox 1996). Thus, 9th millennium BP levels at Halula see the appearance of domesticated crops such as naked wheat (*Triticum aestivum* and/or *T. durum*), hulled wheat such as emmer (*Triticum dicoccum*) and barley (*Hordeum vulgare*) (Molist *et al.* 1995; Willcox 1996; Willcox and Catalá 1996). The cultivars appear to have been introduced from elsewhere. With regard to edible pulses Ladizinsky (1987, 1989) argues that domestication of grain legumes such as lentils was before that of any other crop. Anyway, as in the case of cereals, domestication of grain legumes would have been possible only under cultivation (Zohary 1989).

Information about the environmental conditions during the beginning of agriculture is scarce and indirect. Recent data on climatic conditions within a more precise chronological framework (Baruch and Bottema 1991; Moore and Hillman 1992) are helping to explain the environmental setting during the transition from hunting/gathering to farming communities. The presence of wild rye (and also wild einkorn) at a number of early sites, including Euphrates sites, during the 10th and 11th millennia BP would appear to indicate cooler and moister climatic conditions than today (Hillman *et al.* 1993; Willcox 1996). However no evidence of rye appears in the 9th millennium BP levels at Halula when agriculture was present (Molist *et al.* 1995; Willcox 1996). Indeed the occupation of the aceramic Euphrates sites coincides with the latter part of the period of global warming following the Younger Dryas (Baruch and Bottema 1991). Thus it is probable that present-day temperatures are higher than those which occurred during the Neolithic.

Other archaeobotanical evidence also supports the possibility that environmental conditions during the beginnings of agriculture were more favorable (i.e. cooler and moister) in this region than nowadays. They are based on the former presence of gallery forest species, identified by charcoal analyses, such as ash, vine, elm and plane which, today, are only found much farther north in Turkey and Greece. Similarly, almond, *Pistacia* and deciduous oak, which nowadays only occur at higher altitudes in the region, also suggest that conditions during the Neolithic were cooler and moister (Harlan 1995; Willcox 1996). However, vegetation degradation through human impact, particularly grazing by livestock, rather than climatic change must account for some of the differences between the vegetation of the early Neolithic and that of the present day. This makes it difficult to evaluate precisely the effect of climatic change on the vegetation (Willcox 1996). Indeed archaeobotanical data from Tell Halula levels (less than one millennium younger than other PPN sites of the Euphrates) indicate a shift to the contemporary steppe/weed vegetation.

Summarizing, even when present palaeoclimatology data and archaeological discoveries strongly suggest a more humid environment prevailing in the Near East at the beginnings of the Holocene, much remains to be discovered about the precise nature of the climate during these crucial millennia (see F. Hole, this volume) as well as the cultural conditions of agriculture at the beginnings of domestication. For example there are no reliable data on precipitation (or even water status) for this period (Rossignol-Strick 1993).

For C_3 plants, such as most of the crop plants first cultivated in this region, carbon isotope discrimination (Δ) in crop grains constitutes an integrated record of the ratio of intercellular to atmospheric partial pressure of CO_2 (p_i/p_a) and thus of the water status during the growth of these grains (Farquhar and Richards 1984; Araus and Buxó 1993; Araus *et al.* 1997). Both decreased water availability and increased evapotranspiration cause lower p_i/p_a and thus A in grains because of their effects on stomatal transpiration or photosynthetic capacity (Farquhar and Richards 1984; Romagosa and Araus 1991; Condon *et al.* 1992). Therefore, from the analysis of A of grains it should be possible, in principle, to infer water status during grain-filling (Fig. 1). In this context the measurement

of A from seeds found in archaeological sites has been proposed as a method to evaluate the water status during the growing of these crops (Araus and Buxó 1993; Araus *et al.* 1997). Nevertheless an inherent limitation of the Δ approach would be the difficulty of distinguishing with certainty low (i.e. suboptimal) levels of irrigation from the existence of a wetter climate in the past or the utilization of naturally wetter soils. In the present study the A method is applied to elucidate the water status of different crop plants grown in Tell Halula during a period of about 1000 years between Middle Pre-Pottery Neolithic B (PPNB) and late Neolithic (ca. 8700 to 7700 BP uncalibrated).

Material and methods

Archaeological site and plant material

Tell Halula is situated in northern Syria about 100 km east of Aleppo and 30 km southeast of Membij. This site is on the west river bank, in a subsidiary valley, 4 km from the main Euphrates Valley. The archaeological site comprises Middle and Late PPNB, and late Neolithic (pre-Halaf) and is being excavated by the Universitat Autonoma de Barcelona. The present-day natural vegetation in the region is a degraded steppe, with a total annual rainfall of about 250 mm (Willcox 1996). At present the land above the valley floor is extensively used for dry (i.e. rain-fed) farming of barley, whereas wheat and horticultural crops are only cultivated where irrigation is available.

Samples of seeds of naked wheat (*T. aestivum/durum*), lentil (*Lens orientalis/culinaris*) and flax (*Linum* spp.) were used for stable carbon isotope analysis. They were found in a carbonized state and were gathered from domestic fires, cooking ovens and floors of rooms. Six different stratigraphic levels from the archaeological site were studied. Soil samples were treated using a standard flotation tank in the field with 0.3 mm (flotation) and 2.5 mm (wet) sieves. Plant remains were then dried slowly before transport and sorting of seeds. Material was compared with modern reference material which had been gathered from various locations in the Near East. Palaeobotanical determinations were performed at the Institut de Prehistoire Orientale of the CNRS, Jalès (France) under the supervision of G. Willcox. The three species considered in this study were present throughout the stratigraphic sequence studied. Chronology of archaeological samples, in years before the present (BP), was based on stratigraphic dating and radiocarbon ages. Radiocarbon determinations were performed at Beta Analytic Inc. (Miami, Florida, USA). Dates ranged from ca. 8700 ± 60 BP to 7690 ± 130 BP uncalibrated. Calibrated ages were determined according to Stuiver and Reimer (1986) by using the computer program CALIBTH3. After calibration the range of dates for the material studied was 9550 to 8465 BP. In addition samples from the present time (1997) were taken from hulled barley cultivated near the site.

Carbon isotope analysis

Prior to stable carbon isotope analysis, seed samples were cleaned as reported elsewhere (Araus and Buxó 1993). The $^{13}C/^{12}C$ ratios were determined by mass spectrometric analysis at Isotope Services, Inc., Los Alamos, New Mexico, USA. Results are expressed as $\delta^{13}C$ values, where:

$$\delta^{13}C(‰) = [(R\ sample/R\ standard) - 1] \times 1000$$

R being the $^{13}C/^{12}C$ ratio. A secondary standard calibrated against Peedee belemnite (PDB) carbonate was used for comparison. Sample sizes of 5-10 mg were used. The precision of analysis was less than 0.10‰. The potential effect of carbonization on $\delta^{13}C$ of archaeological grains was ignored as reported before (Marino and DeNiro 1987; Araus *et al.* 1997).

Discrimination (Δ) against ^{13}C relative to air was calculated from δ_a and δ_p, where a and p refer to air and plant respectively (Fig. 1); as follows (Farquhar *et al.* 1989):

$$\Delta = \frac{\delta_a \quad \delta_p}{1 + \delta_p}$$

On the PDB scale, δ_a currently has a value of approximately -8.00‰. For calculation of Δ values of grain samples from the archaeological site, δ_a values were inferred from the work of Marino *et al.* (1992) as reported elsewhere (Araus and Buxó 1993).

Fig. 1. Stable carbon isotope composition ($\delta^{13}C$) of plant tissues is the result of two different kinds of

factor: (1) the isotopic composition of the carbon source (surrounding air, δ_a) used by the plant during photosynthesis, and (2) for most plant species (C$_3$ plants), the water status during growth. The effect of δ_a on δ^{13}C can be eliminated by calculating the carbon isotope discrimination (Δ). Therefore Δ of plant material reflects the water regime during its growth. In principle this is applicable either to samples from currently growing plant material or to plant remains from archaeological sites.
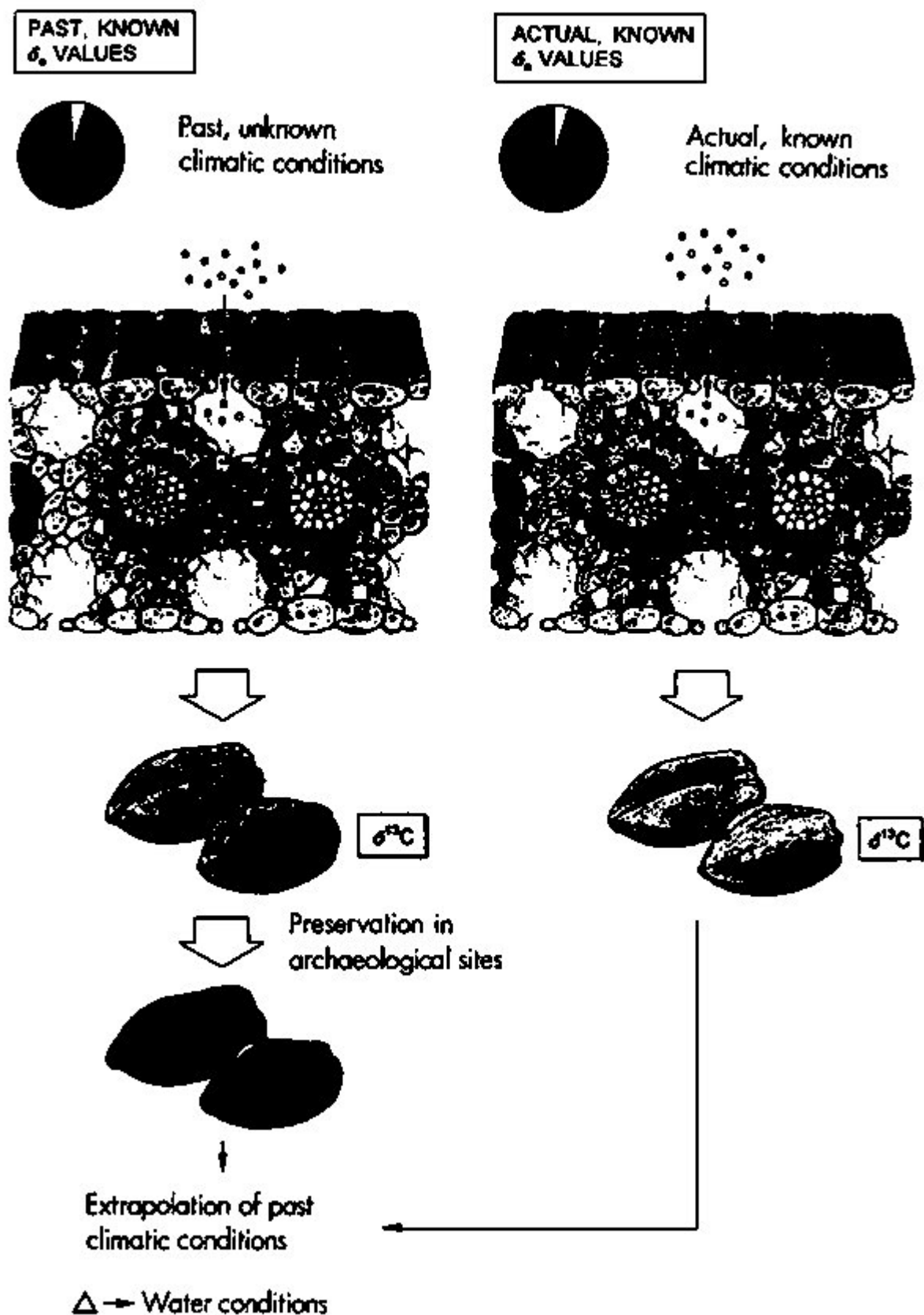
Results and discussion

Except for two samples (one of wheat and the other of lentil) all the seeds studied showed carbon isotope

discrimination (Δ) values greater than 16‰, reaching 20‰ for some samples of flax (Fig. 2). These values of Δ are very high for rain-fed crops growing under Mediterranean conditions. For example, whereas Δ values for wheat kernels were around 17‰ during the period studied (Fig. 3), it has been reported that kernel Δ of 17.5 ‰ and higher would indicate growing conditions resembling those grown under full irrigation (Araus et al. 1997). Indeed the water regime during grain-filling strongly affects the Δ values of mature kernels (Romagosa and Araus 1991; Condon et al. 1992; Araus et al. 1997, 1998). Thus, under the usual rain-fed conditions in the western Mediterranean basin, the relatively low precipitation and high evapotranspiration at the time of grain-filling led to significantly lower A values in mature kernels than in those grown under irrigated conditions. In the same way, the Δ values of wheat were much higher than those reported in wheat crops cultivated under rain-fed conditions in northwest Syria during the 1995/96 season (Araus et al. 1998) in environments with similar (Breda) or somewhat higher (Tel Hadya) rainfall than Tell Halula. Thus, mean ± SD values for Breda and Tel Hadya were 14.0 ± 0.4‰ and 15.3 ± 0.4‰, respectively. These values were clearly below those measured in the archaeological seeds (Fig. 2).

Samples from hulled barley kernels cultivated in seven different places during the 1996/97 season around the archaeological site were also analyzed. These barley crops grow without significant (if any) chemical nitrogen fertilization, as inferred from the low total nitrogen content and the high proportion of stable isotope ^{15}N ($\delta^{15}N$) in kernels (Amaro et al. 1995), a situation similar to that expected in ancient agriculture. Mean ± SE of Δ was 16.02±0.19‰. This value is again clearly below Δ values for all the archaeological seeds. Moreover, under present conditions, Δ of wheat would be even lower. Considering that barley attains maturity at least 2-3 weeks earlier than wheat, the grain-filling period for barley usually takes place under wetter conditions than those that could be expected for wheat. Indeed this difference in phenology between both crops is the reason why, among cereals, barley is more commonly cultivated under rain-fed conditions in areas with conditions comparable to those which predominate in Tell Halula at present.

These results strongly suggest that, during the period studied, wheat was cultivated at Tell Halula under much wetter conditions than could be expected from present-day conditions. The presence of flax and its very high Δ values also support this conclusion. Cultivation under more humid conditions could have been possible owing to more humid environmental conditions prevailing at that time or by planting in alluvial areas (Bar-Yosef and Kislev 1989). Another possibility lies in the existence of irrigation practices. Indeed one indirect method to assess the presence of ancient irrigation takes into consideration the development of weeds; for example, from the size of charred flax seeds which occurred in an archaeological assemblage of plant remains (Helbaek 1960). However, even when flax seeds were very abundant in all the stratigraphic levels studied at Tell Halula their length did not reach 3.0 mm which has been proposed as the minimum size for domesticated plants.

In the case of wheat, although Δ values of archaeological kernels were higher than those of kernels cultivated at present because of the wetter conditions, they were still lower than typical values of irrigation. In fact, Δ seems to depend on the water accumulated during grain-filling on a logarithmic basis (Araus et al. 1997). Therefore, Δ values slightly lower than those reported as typical of irrigated crops under Mediterranean conditions will be associated with considerably lower amounts of water during grain-filling. For example a value of Δ 0.5 ‰, lower than that typical of irrigated wheat (17.5 ‰), would correspond to an amount of water during grain-filling about 30% lower than that of irrigated crops (Araus et al. 1997). Of course any condition between rain-fed and full irrigation (i.e. irrigation support) would produce kernels with A values below those of full irrigation.

Fig. 2. Carbon isotope discrimination of durum wheat, lentil and flax seeds found in six different stratigraphic levels of Tell Halula ranging from Middle PPNB (ca. 8700 ± 60 BP uncalibrated) to late Neolithic (ca. 7690 ± 130 BP uncalibrated). The Δ values from present-day (1996) mature kernels of durum wheat cultivated under rain-fed conditions in northwest Syria in environments with similar (Breda) or somewhat higher (Tel Hadya) precipitation than Tell Halula are presented for comparison. For these two environments values presented are means ± SD of 144 genotypes and two plots each (Araus et al. 1998).
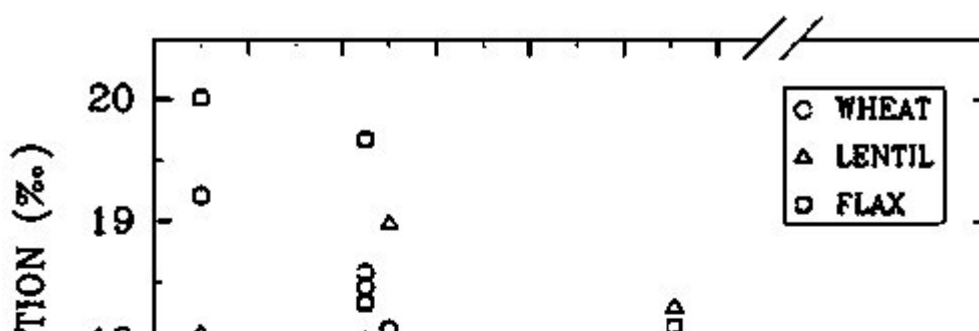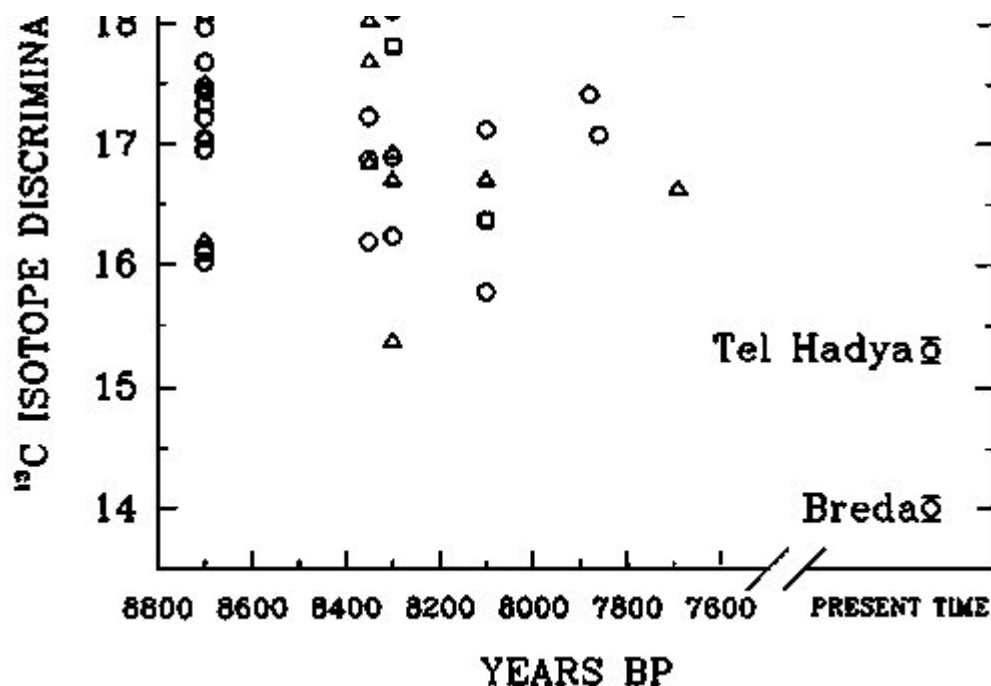
Fig. 3. Mean ± SE of Δ values of durum wheat, lentil and flax seeds found in stratigraphic levels of Tell Halula corresponding to Middle PPNB (M-PPNB), Late PPNB (L-PPNB) and late Neolithic (L-N). Means with different letters are significantly different (P ≤ 0.05) by Duncan's comparison test.
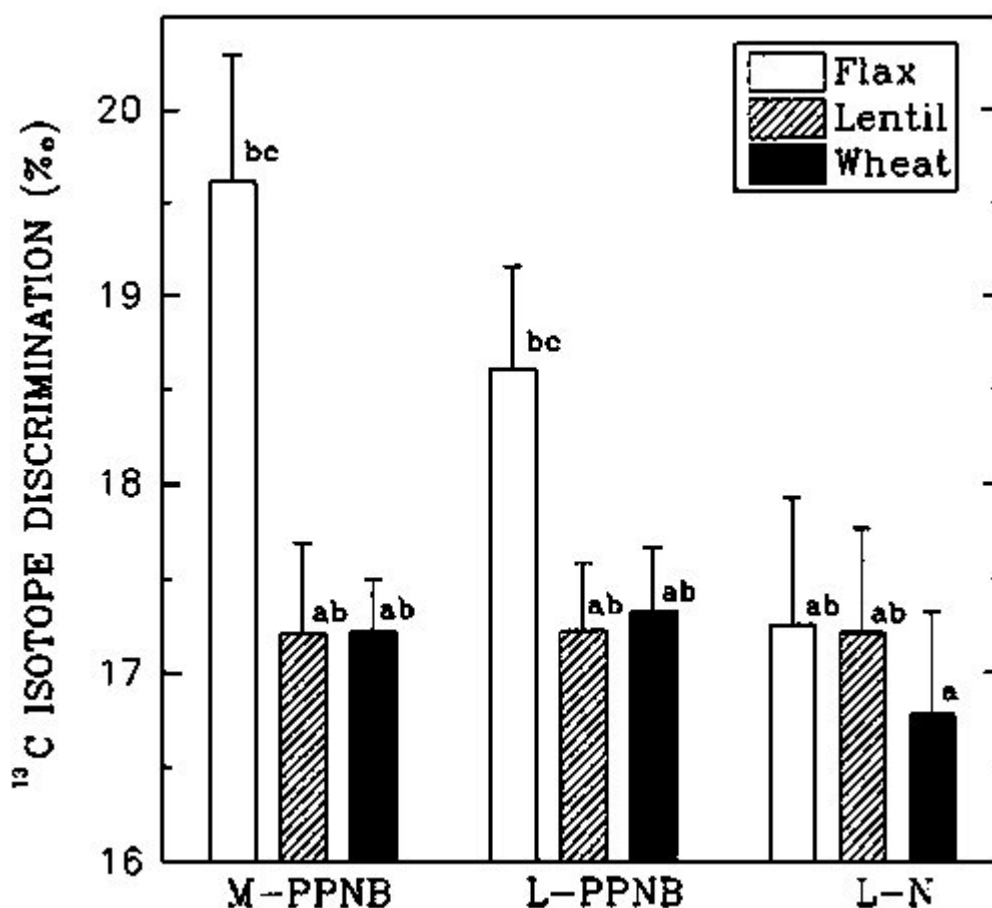
Alternatively, as pointed out above, the exploitation of naturally moist soils (without evidence of irrigation) is largely evidenced in early agricultural sites (Bar-Yosef and Kislev 1989). A high water level in the soil could explain, in turn, such high Δ values in the absence of irrigation. Indeed, if the information of early agricultural sites in the Near East (Bar-Yosef and Kislev 1989) may be considered as a guide, it could be assumed that cultivation whenever possible was based on sowing on alluvial fans and terraces as well as on the edges of freshwater swamps where the water table was always high and the soil fertilized by silt deposited by periodic floods. However, as yet there is no evidence for irrigation (Bar-Yosef and Kislev 1989; Hillman and Davies 1990).

Willcox (1996) notes that the presence of charcoal of ash, vine, maple, plane, alder and elm from the gallery forest, and wild rye, wild einkorn, deciduous oak, wild almond, *Pistacia* and *Pyrus* from the hinterland, indicates cooler conditions in the middle Euphrates region at the beginning of agriculture. Particularly in Halula the presence of *Quercus, Amygdalus, Pistacia* and *Olea europaea* during the PPNB suggests that climate was much more humid than at present (Willcox and Catalá 1996). However the present-day natural vegetation corresponding to a degraded steppe could be the consequence of human effect on the landscape. Thus, annual weed plants usually associated with open landscape, due to the cultivation of cereals or other plants, were already present in the same soil samples where wheat, lentil and flax appeared. In addition they occur throughout the stratigraphic sequence studied. Among these annual plants it is worth mentioning the genera *Centaurea, Astragalus, Glaucium, Galium, Lithospermum, Teucrium, Sherardia, Fumaria* and *Rumex.* Expansion of cultivation as well as the great development of extensive goat and sheep pastoralism, could be responsible for this increase in landscape degradation. Nevertheless, in comparison with the contemporary steppe vegetation, the archaeobotanical results indicate a moister, cooler, more continental vegetation found today at higher altitudes and more northerly latitudes (Willcox 1996).

Regarding the possible effect of past climate on Δ, not only an overall higher precipitation (and perhaps a lower evapotranspiration), but also the seasonal distribution of precipitation, would be involved. Thus at the site of Mureybit on the Euphrates it has been reported that about 8000 BP Poaceae pollen was, in relative terms, much more abundant than today (El-Moslimany 1994). This suggests that in the middle Euphrates region summer precipitation was much higher than today. A shift throughout the region to dominant winter rainfall (typical of Mediterranean climates) would occur after 6000 BP (El-Moslimany 1994). Because for durum wheat and flax, seed formation takes place in late spring and early summer, any increase in precipitation during this period, even when total accumulated rainfall during cultivation does not vary, would eventually lead to higher Δ on seeds.

For each plant species, means of Δ for the samples found in the different stratigraphic levels corresponding to Middle PPNB and Late PPNB and late Neolithic (pre-Halaf culture) were plotted (Fig. 3). Flax seeds showed higher values of Δ than wheat kernels and lentil seeds during the Middle and Late PPNB. Lentil seeds also tended to show higher Δ values than wheat during the late Neolithic. This could reflect the growth habit, lentils being less determinate plants than cereals (Araus *et al.* 1997).

As a general trend Δ values tended to decrease with time, particularly those of flax. Flax is reported to be an indicator of either high precipitation (see F. Hole, this volume) or irrigation practices (Helbaek 1960). This decrease in Δ suggests a gradual change in climate with an evolution to drier conditions. The first evidence of domesticated plants (cereals) on Tell Halula (ca. 10,000 BP calibrated) appears a full 1000 years after the Climatic Optimum was already established (Becker *et al.* 1991). The progressive attenuation of the Climatic Optimum until around 6000 years ago, when climatic conditions not far from those prevailing at present were established throughout the Near East (Roberts and Wright 1993), would agree with this tendency on Δ values.

To summarize, present results strongly suggest that during the period studied, wheat and lentil were cultivated at Tell Halula under much wetter conditions than today. The presence of flax and its very high Δ values also support this conclusion. Cultivation under wetter conditions could have been possible owing either to more humid environmental conditions prevailing at this time, or planting in alluvial areas, or a combination of both.

Acknowledgments

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Part 2. Near Eastern Crop Diversity and its Global Migration

Diversity of Major Cultivated Plants Domesticated in the Near East - A.B. Damania

Our fathers planted gardens long ago...
Whose fruits we reap with joy today;
Their labor constitutes a debt we owe...
Which to our heirs we must repay;
For all crops sown in any land...
Are destined for a future man.
Arab Poet - Nizami

Introduction

Alexander von Humboldt was probably the first author to refer to the question of origins of crops in his work *Essai sur la Géographie des Plantes* in 1807. Possible reasons for humans to have abandoned their hunting/gathering ways and settled down to the sedentary pastoral life of a cultivator have been discussed by several authors, among them Ucko and Dimbleby (1969), Harlan *et al.* (1976a), Zeven and de Wet (1982), Smith (1995), Harris (1996) and Diamond (1997).

Alphonse de Candolle, in his 1882 book *Origine de Plantes Cultivées,* was among the first to indicate regions where plant domestication may have taken place: China, Southwest Asia including Egypt, and Tropical Asia. In 1926, during the Fifth International Genetics Congress in Berlin, Vavilov expounded his theory of centers of origin of crop plants for the first time. The centers recognized by Vavilov were: China, India, Indo-Malaya, Central Asia, Near East, the Mediterranean, Ethiopia, Southern Mexico and Central America, South America and Chile. Vavilov continued to work on his theory until his death in 1943.

Harlan *et al.* (1976b) refer to the Near East as the "center of agricultural innovation" where barley was the first crop to be domesticated followed by wheat. Later the other 'founder crops' such as pea, lentil, vetch, faba bean, flax, tree and vine fruits were domesticated and the entire system moved out of the nuclear area together with an array of agricultural techniques. The system spread, moving along the shores of the Mediterranean and up the banks of the Danube River and down the Rhine, eastward to the Indus and northern India and southward across Arabia, the Yemen and into the Ethiopian plateau. It did not proceed further down into tropical Africa. It reached China in the second half of the 2nd millennium BC (Harlan *et al.* 1976b).

Arab geographers, authors of garden books and other writers from the 10th century AD onward tell about a countryside in the Islamic world that had changed significantly since ancient times (Watson 1983). The 'new' crops were mostly fruit trees, grains other than wheat and barley, and vegetables and several others. These introductions greatly increased the diversity of crops that appealed to different tastes. Watson (1983) gives a few examples of the diversity available at that time: the writer Al-Jahiz in the 9th century AD stated that there were 360 varieties of dates (*Phoenix dactylifera*) to be found on sale in the market at Basra in Iraq, while in the following century Ibn Rusta stated there were 78 kinds of grapes (*Vitis vinifera*) being grown in the vicinity of San'a (Yemen). Al-Ansari, writing about a small town in North Africa, stated that in the year 1400 AD there were 65 kinds of grapes, 36 kinds of pears, 28 kinds of figs, 16 kinds of apricots, and so on. The Arab conquests during the 7th and 8th centuries AD greatly facilitated the introduction of new varieties of crops in the Near East.

This paper focuses on the crop diversity of the above region, an important area recognized by most authors as one of the major centers of origins of crop plants and genetic diversity as well as innovation of agricultural

techniques. However, this Vavilovian center overlaps in places with the Mediterranean Center and hence crops of the latter with wide distribution in the Near East are also included for comprehensiveness. Much of the information given here has been adapted from Zeven and de Wet (1982) and Vavilov (1992). Brief descriptions of selected major crops which have their greatest diversity and/or were domesticated in this region are given below in alphabetical order of their botanical families.

Major crop plants domesticated in the Near East

The genus *Allium* (Family: Alliaceae) includes the common garlic and the onion which form the very basis of Asian and Mediterranean food preparations. *Allium ampeloprasum* or sweet leek (Levant garlic) is found all over Europe, Asia Minor and North Africa. Its presence in the Channel Islands and western France is thought to represent relics of former cultivation rather than recent introduction. According to Vavilov, the primary center of origin of onion is in Central Asia and that of leek in the Near East and the Mediterranean. *Allium ascalonicum* or shallot is closely related to *A. deserti-syriaci* from the deserts of Syria and Iraq. It has also been described as a variant of *A. cepa,* the common onion. *Allium kurrat* or salad leek originated in Sinai and is grown in the Nile delta, Palestine and Arabia for its leaves. *Allium porrum* or leek has its greatest diversity in Asia Minor and is derived from *A. ampeloprasum,* its wild progenitor. And finally, *A. sativum* or garlic has its primary center in Central Asia but a secondary center in Southwest Asia. Wild *Allium* species often invade cereal fields all over Southwest Asia. They can be distinguished quite simply by their deep purple or light green inflorescence.

Pistacia vera (Anacardiaceae) or pistachio is native to the Near East and Southwest Asia where it has been cultivated for over 4000 years. Kernels of naturally occurring forms are known from sites long before that. Secondary centers of diversity have developed in Iran and Syria. Relic populations of former extensive cultivation are found in Turkmenistan and Kyrgyzstan. Another species, *P. terebinthus,* is used as an alternative pollinator and as rootstock on which young male and female pistachio trees can be grafted.

Carthamus tinctorius (Asteraceae) or safflower has its origin in the Near East according to Ashri and Knowles (1960) since the cultivated form is similar to two closely related species: *C. flavescens* found in Turkey, Syria and Lebanon (usually as a weed in wheat fields), and *C. palaestinus* found in the deserts of Western Iraq and Palestine (see McCorriston, this volume). In these areas introgression between the wild and cultivated forms may still occur, leading to an exchange of genes. One species in the group, *C. leucocaulos,* is distinctly different from other species. Stems are smooth, head size is small, colored flowers are light purple or light pink instead of purple, and self-fertility is high. It is endemic to the Aegean Islands, but has been introduced to southern Europe, Australia and the USA. *Carthamus divaricatus,* which is endemic to Libya, is the only species which is morphologically distinct. It has horizontal branches; strongly divaricate outer involucral bracts; yellow, purple and white flowers; yellow pollen, and dark purple striped anthers. *Carthamus oxyacanthus,* found in continental areas from western Iraq through to northwestern India, and extending northward to southern former USSR, in all areas is a very serious weed. Two other species also found are *C. gypsicolus,* similar to *C. oxyacanthus* and restricted to the former USSR, and *C. curdicus,* with characteristics of both *C. gypsicolus* and *C. flavescens* and restricted to northern Iraq. All the above have 12 pairs of chromosomes. There are two species with 32 pairs of chromosomes, *C. turkestanicus* and *C. baeticus. Carthamus turkestanicus* ranges from Turkey in the west to northern Pakistan and Kashmir, India in the east, with presumably introduced populations in Ethiopia. *Carthamus baeticus* may be found around the entire Mediterranean Sea and in its islands. All wild species of safflower are spiny weeds, some of them very serious because they occupy fields sown to other crops. Others are more prevalent in roadsides and waste places. They are characterized by yellow flowers, although white flowers with yellow pollen grains are not unknown. At an early stage in its evolution, *C. tinctorius* spread to Egypt, Ethiopia, southern Europe, South Asia and the Far East where distinctive types have evolved.

Several wild *Beta* spp. (Chenopodiaceae), which are relatives of *Beta vulgaris* or beetroot, are widespread in this region. Among them are *B. corolliflora* found in Turkey, Azerbaijan, Georgia and in parts of Iran. It is known for its resistance to frost and is often used in crosses with cultivated species. *Beta intermedia* is said to have evolved as a result of a cross between *B. lomatogona* and *B. trigyna,* two other wild forms. *Beta lomatogona* is itself a weed found all over Asia Minor and *B. trigyna* is found around the Black Sea with a few samples found as far as the Caspian Sea, Ukraine and Hungary. *Beta macrorrhiza* is found at higher altitudes in the mountains of Iran, Turkish Armenia near Lake Van and the Caucasus. It is a cold-resistant species, sweet tasting with a white pulp. The sugar beet, *B. vulgaris,* has its origins in the western Mediterranean.

Spinacia oleracea (Chenopodiaceae) or spinach is a native of Southwest Asia but has become well established almost all over the world, having been introduced in Europe, the Americas and the Far East.

Cichorium intybus (Compositae) or chicory is a perennial salad plant native to the parts of southern Europe bordering on the Mediterranean. It was cultivated in Greek and Roman times and has become naturalized in parts of North America. *Cichorium endivia* or endive is indigenous to the eastern Mediterranean.

Cynara scolymus (Compositae) or artichoke was probably developed from its wild progenitor *C. cardunculus,* a native of the Mediterranean whose stalks and leaves are edible. There are several words for the plant in the Berber language, which indicates the possibility of its origin in the Maghreb. It moved in to Europe in the Middle Ages.

Lactuca sativa (Compositae) or lettuce evolved as a natural selection from its closest wild progenitor, *L. serriola,* which is a prickly biennial of the temperate regions (Purseglove 1968). *Lactuca sativa* originated in the eastern Mediterranean about 7000 BP, most likely in Egypt when the climate of that part of northeastern Africa was not as dry as it is today. Lettuce was a common oilseed crop in Upper Egypt as far back as 6500 BP as depicted by rosettes of a tall, large vegetable with subulate leaves painted on the walls of tombs at Thebes (2500 BC). The presence of latex in primitive lettuce also marked the plant as a fertility symbol. Unfortunately, the available illustrated record found in ancient monuments is not complemented by dry or carbonized remains of leaves or seed of this crop in Egypt.

Early human selection for non-shattering seed heads, late flowering, non-prickly leaves, decrease in latex content, and hearting character (the tendency of leaves to congregate in layers in a heart-shaped head) is said to have led to its domestication as a leafy salad vegetable. Lettuce reached China around the 7th century AD where a special cultivar of the asparagus type (*L. Serriola* f. *integrifolia*) was developed and reported by Fuchs in 1543 from Sinkiang. The local name of this variety is 'usum' or 'on-sen'. According to Vavilov (1992) this form of lettuce is practically unknown in Southwest Asia.

Cornus mas (Cornaceae) or Cornelian cherry is found all over Caucasia and Asia Minor as an underbrush of deciduous forests. The fruits are edible and are used to produce an alcoholic beverage, vin de Cornouille. The fruits are of great antiquity and have been reported from archaeological sites over 10,000 BP in 1991 from the PPNB site of Nevali Çori, near Urfa, in southeastern Turkey (see Pasternak, this volume).

Corylus avellana (Corylaceae) or European hazelnut has its primary center in the Caucasus where a number of other *Corylus* species are also found. However, it was domesticated relatively recently in 17th century Italy. *Corylus colurna* or Turkish hazelnut or cob nut is cultivated in Turkey for export and also used as rootstock for *C. avellana* since it possesses resistance to several diseases. Hybrids between the two are called 'trazels'. *Corylus maxima* or filbert nut tree is native to West Asia, southeast Europe and the Caucasus.

Brassica oleracea (Cruciferae) or cabbage has a secondary center in Asia Minor where convar. *oleracea* and *capitata* are found. There are wild as well as cultivated forms. Some of the wild inedible forms are also used as ornamentals. *Brassica oleracea* var. *botrytis* or cauliflower is a native of the eastern Mediterranean

Cucumis melo (Cucurbitaceae) or musk melon (cantaloupe) has its origins in Africa but has an important secondary center in the Near East where some of the sweetest fruits are found. Similarly, *Cucumis sativus* or cucumber, a native of India, also has a secondary center in this region and cucumbers are part of all Near Eastern cuisines from Turkey through to Iran and Afghanistan. In Iran tender cucumbers are eaten with yogurt (mást-khiyár) on a daily basis.

Ricinus communis (Euphorbiaceae) or castor was known to the ancient Egyptians as far back as 6000 BP. Its oil was used as an illuminant. Although it originated in Africa, it grows wild in the Yemen and all of the Near and Middle East. It was taken at an early date to India. Today castor oil has great commercial value in the paint and lubricant manufacture industries. The oil also has been used as a purgative (home remedy) since ancient times.

Castanea sativa (Fagaceae) or chestnut is found from southern Italy to Asia Minor and western Georgia in the former USSR. It was introduced to southern Europe by the Greeks and the Romans, and then transported to northern Europe and Britain. Nuts are roasted, the shells removed and the insides eaten or used in confectionery.

A number of *Aegilops* spp. (Gramineae) or goatgrass are native to West Asia and the Near East. *Aegilops* was known to the ancient Greeks and the name is related to its supposed healing properties of an eye disease from which goats suffer (van Slageren 1994). *Ae. columnaris* is spread from Turkey through Iraq, Iran and Caucasia. It is a common weed found in and on the borders of fields. *Ae. crassa* is also found in Turkey, Syria, Palestine, Iraq, Iran and Afghanistan. *Ae. cylindrica* is found in the Balkan peninsula, Crete, Turkey, Caucasia, Armenia, Azerbaijan, Iran, Iraq and Afghanistan. It is a weed in fallow fields and along slopes of hillsides. *Ae. kotschyi* is found from North Africa across Palestine, Iraq, Iran, Afghanistan and Caucasia. *Ae. laurentii* has a wider distribution, i.e. from southern Europe, former USSR, Turkey, Palestine, Iraq and Iran. *Ae. mutica* is restricted somewhat to Armenia and Anatolia in Turkey and *Ae. ovata* is just the opposite, being found all over the Mediterranean, Palestine, Syria, Lebanon, Turkey, Iraq, Iran and Afghanistan. A weed of cultivated wheat fields, it has a male-sterilization action on the nucleus of *Triticum aestivum* and *T. turgidum*. *Ae. speltoides* has its primary center in southern Turkey and northern Syria and Iraq. It is less common in places bordering the above. It is often found growing with wild wheat (*T. boeoticum*) in southern Turkey and northern Syria. *Ae. triaristata* is

found in the Mediterranean, West Asia, Iraq, Iran and southern parts of the former USSR. *Ae. triuncialis* is all over the Mediterranean area, Turkey, Palestine, Syria, Lebanon, Iraq, Iran, Turkmenistan and Afghanistan. It has been suggested that it is a hybrid between female *Ae. caudata* × male *Ae. umbellulata* that originated in West Asia. *Ae. umbellulata,* on the other hand, occurs on moist steppe, dry slopes of hills, and is a weed in cultivated fields in the Greek islands, Turkey, northern Syria, Iraq, northwestern Iran and Transcaucasia. It is resistant to leaf rust and hence used often in wheat breeding. Some *Aegilops* spp. cross readily with others, e.g. *Ae. sharonensis,* whereas others are cross-pollinators which readily produce hybrids. *Aegilops* spp. that occur on the borders of cultivated *Triticum* fields often exchange genes although the hybrids are mostly sterile.

Hordeum vulgare (Gramineae) or barley is one of the oldest crops to be domesticated in this region, from its wild progenitor *H. spontaneum.* The wild progenitor of barley is found in the eastern Mediterranean, West Asia, and as far as Turkmenia and Afghanistan. Domestication of barley is said to have taken place around 9000 BP in the Fertile Crescent. However, grains of barley have been found in Egyptian tombs dating from 15,000 BP. But it would be difficult to distinguish between wild *H. spontaneum* and its domesticated form from looking at carbonized remains. Other finds include those discovered in Cayönü in Turkey dating from 9000 BP (Braidwood *et al.* 1969). The domesticated barley spread through the Mediterranean to Rome and beyond as well as eastwards through Iran and Afghanistan into India and from India to China through Tibet. There are several forms but they all have a brittle rachis and very long awns. For some time *H. agriocrithon,* a brittle rachis six-row form first reported from Tibet, was thought to be the progenitor of six-row barley. But later this theory was discounted as such brittle rachis forms were also found where *H. spontaneum* came into contact with six-row barley. These forms mature about two weeks before the cultivated six-row barley and occur as weeds in barley fields all over Tibet. They are easily distinguished from cultivated forms by their purple to black spikes. However, *H. agriocrithon,* unlike *H. spontaneum,* has not yet been found growing by itself in the wild state away from cultivated fields.

Avena sativa (Gramineae) or oats. Two hexaploid oats have been recognized: *A. sativa* and *A. byzanthina. Avena sterilis,* the wild oat, is recognized as the progenitor with its center of diversity in the Near East and the Mediterranean. Wild oats are perpetual invaders of cereal fields in Southwest Asia and elsewhere. Other wild species found in this region are: *A. damascena* (found in an area 60 km north of Damascus in Syria), *A. clauda, A. longiglumis, A. moroccana* (found in Morocco and sometimes mistaken for *A. sterilis*) and *A. strigosa* (black oat, found all over the Mediterranean).

Secale cereale (Gramineae) or rye has its primary center of origin in northeastern Turkey and northwestern Iran. A secondary center has been suggested in Afghanistan from where the crop may have migrated to central Asia and Europe. A number of genetic variants exist, one of which (*S. segetale*) evolved into the annual wild rye weed (see Jaaska, this volume). Hybridization between cultivated wheat and rye has resulted in the triticales which have resistance to several diseases. Cultivated rye is known from the Neolithic age in Austria, but it seems to have become widespread in Europe only after the Bronze Age.

Secale montanum (Gramineae) or mountain rye is a perennial species found in the central Atlas Mountains of Morocco, Sierra Nevada Mountains of Spain, Italy, Sicily, Yugoslavia, Greece, Lebanon, Turkey, Iran and Iraq. It is highly polymorphic and crosses readily with other *Secale* spp., producing several weedy forms and varieties. Other species include *S. silvestre* and *S. vavilovii,* which occurs on the slopes of Mt. Ararat and along the banks of the Araks River.

Sorghum halepense (Gramineae) or Johnson grass, a relative of the cultivated sorghum (*S. bicolor*), is found from the Mediterranean up to Pakistan. It is a rhizomatous perennial first identified near Aleppo (Halep) in Syria. It occurs as a weed on the borders or in cereal fields. It is a source of disease resistance for cultivated sorghum with which it crosses readily.

Triticum aestivum (Gramineae) or common wheat or bread wheat has its primary center in Transcaucasia and adjacent areas and is by far the most important crop that this region has given the world (see Dvorak, this volume). Natural cross-fertilization still takes place between wild and cultivated *Triticum* spp. and many authors believe that wheat is still evolving. It is said to have arisen as a result of a cross between *T. dicoccum* (emmer wheat) and *Ae. squarrosa.* This cross must have taken place after emmer evolved from its wild progenitor, *T. dicoccoides,* in the area south of the Caspian Sea. Several other hexaploid forms eventually evolved and they are as follows: *T. vavilovii,* a species peculiar to Armenia, *T. spelta* (spelt wheat) is still cultivated in parts of Spain, *T. macha* (macha wheat), *T. compactum* (club wheat, was grown in Syria until the last century and volunteers can still be observed in cultivated fields of *T. aestivum*) and *T. sphaerococcum* (dwarf shot wheat with globoid grains native to India, where it is still grown in small pockets). A secondary center of diversity for hexaploid wheat developed in the Hindu Kush Mountains where the crop encountered a physical barrier to further migration, i.e. the theory of peripheral diversity (Yamashita 1980).

Triticum monococcum (Gramineae) or einkorn was domesticated in the Fertile Crescent from one of its wild

progenitors, *T. boeoticum* or *T. urartu.* Its earliest recorded archaeological find is from the site at Ali Kosh in Iraq dating from 8500 BP. *Triticum boeoticum* subsp. *thaoudar,* the wild progenitor with two grains and two awns, has been reported growing in wild stands from Diyarbakir in Turkey and remains have been found from the site at D'jade on the Euphrates where it was grown and harvested in the green state. *Triticum monococcum,* although considered obsolete, is still cultivated as a feed for poultry and swine in the mountainous villages in Italy, Spain and Turkey and elsewhere.

Triticum timopheevi (Gramineae) consists of two subspecies: *araraticum* and *timopheevi.* The former grows wild in the northeastern arc of the Fertile Crescent. The latter species, however, is part of what is termed the Zanduri wheat, cultivated in Georgia in the former USSR. This type of wheat is formed by diploid einkorn, tetraploid *timopheevi* and hexaploid *zhukovskyii* wheats. Neither subspecies crosses readily with other wheats.

Triticum dicoccoides (Gramineae) or wild emmer is found all over the Fertile Crescent. Recently wild stands have been reported from Suweida province south of Damascus in Syria. Wild emmer has been used in crosses with cultivated tetraploid wheat to improve disease resistance of the plant and protein content of the grain. Several cultivated tetraploid wheat forms may have been derived from wild emmer: *T. dicoccum* (emmer wheat), *T. turgidum* (poulard wheat), *T. carthlicum* (Persian wheat), *T. durum* (macaroni wheat), *T. polonicum* (Polish wheat) and includes *T. ispahanicum, T. turanicum* (Khurasan wheat) and *T. turgidum* subsp. *turgidum* (English wheat).

Triticum dicoccum (Gramineae) or emmer wheat is, according to some authors, the oldest cultivated wheat, being domesticated in the Fertile Crescent around 10,000 BP. Until recently, it was cultivated in large quantities in Ethiopia (the secondary center of diversity for tetraploid wheats), Iran, eastern Turkey, Transcaucasia, Volga Basin, Yugoslavia, Czechoslovakia, Italy, Spain and India. It was seen from frescoes and wall paintings at Thebes and Luxor that *T. dicoccum* was the favored cereal used for bread-making in Egypt. But today its cultivation is on a decline and it can be found only in small pockets of traditional farming communities in the above areas. In India it is called 'khapli' wheat and is now grown only in limited areas in the state of Rajasthan.

Triticum durum (Gramineae) or macaroni wheat is cultivated all over West Asia and North Africa (WANA) and the Mediterranean. In fact, 80% of all the durum wheat grown in the world is cultivated in this region. It is rarely grown outside the WANA region in the Old World. Its price in the world market is higher than bread wheat because of its great demand in the making of pasta dishes in Italy and elsewhere. Ancient texts speak of the possibility of storing durum wheat over long periods because of the low water content of its grains.

Triticum zhukovskyi (Gramineae) or Zanduri wheat is cultivated in western Georgia in the former USSR. It is a hexaploid with a unique genome formula. The designation 'Zanduri', however, is reserved for a mixture of *T. monococcum, T. timopheevi* subsp. and *T. zhukovskyi.*

Cicer arietinum (Leguminosae) or chickpea, also referred to as garbanzo, occurs in two forms: the Mediterranean type (plants with green stem, white flower, owl-head shaped and salmon-white seeds) and the desi type (plants with anthocyanin in the stem and leaves and small seeds with an angular shape and darker color). *Cicer reticulatum,* a wild annual species found in Turkey, could be the wild progenitor since it produces fertile progenies when crossed with cultivated chickpea.

Lens esculentum (Leguminosae) or lentil. The genus *Lens* comprises two species: (1) *L. culinaris* (syn. *Lens esculentum*)*,* which includes three subspecies - *culinaris* (cultivated lentil), and the wild *orientalis* and *odemensis,* and (2) *L. nigricans,* with subspp. *nigricans* and *ervoides.*

The cultivated lentil has been domesticated from its wild progenitor subsp. *orientalis* (see Erskine, this volume). Wild lentils occur from western Europe (Spain and Portugal) to central Asia. According to Harlan (1951) there is a microcenter of diversity for lentils in Turkey.

Lathyrus sativus (Leguminosae) or grass pea was domesticated in West Asia with a center of diversity in the Mediterranean region.

Lathyrus tingitanus (Leguminosae) or Tangier pea has a microcenter of diversity in Morocco where it is cultivated as a winter annual.

Lupinus albus (Leguminosae) or white lupin is found wild in western Turkey but may have been domesticated in the Balkans. Other lupins from the Mediterranean area are: *L. angustifolius, L. cosentini, L. luteus, L. pilosus* and *L. termis.* Egyptian lupin has been found in Palestine and Egypt since ancient times. The seeds contain an alkaloid which has to be neutralized before consumption.

Medicago sativa (Leguminosae) or alfalfa evolved around the Caspian Sea where it occurs as a wild plant. It is

believed that it was the first plant to be cultivated as a forage crop to provide feed for horses and cattle. The Greeks came across alfalfa being used to feed the horses of the mighty Persian cavalry of Darius III around 350 BC. The Greeks quickly adopted the crop for their own use and it spread later into southern Italy and Europe and subsequently to other parts of the world. Several wild *Medicago* species occur in West Asia: *Medicago cancellata,* which is used as a gene source for adaptation of *M. sativa* to poor soils, *Medicago dzhawakhetica,* found in Georgia and parts of Asia Minor, and *M. glutinosa,* found in the Caucasus and also used as a gene source for crop improvement.

Pisum sativum (Leguminosae) or pea was domesticated from the wild *P. humile,* the latter being common in northern Iraq, Jordan, Syria, northwestern Iran, Palestine, Turkey and Cyprus. The crop reached the Greeks through the Black Sea and went eastwards to India and China via the Himalayan trade routes passing through Tibet. *Pisum elatius* is another wild form which is found all over the Near East and in southern Italy and Sardinia. It can also be found in scattered places in North Africa.

Trifolium ambiguum (Leguminosae) or Caucasian clover is found in Caucasia, Crimea and Turkey. It is a very valuable fodder plant. Material taken from Crimea to Australia gave rise to cultivars which can withstand long periods of flooding.

Trifolium israeliticum (Leguminosae) is a forage species reported from northern Palestine.

Trigonella fbenum-graecum (Leguminosae) or fenugreek probably also evolved in West Asia, but is cultivated in southern Europe, North Africa and India as a fodder crop. In India the seeds are also eaten and used in traditional medicine.

Vicia sativa (Leguminosae) or common vetch has a great variation in form, chromosome number and karyotype. Zohary and Plitmann (1979) described seven subspecies as follows: *sativa, macrocarpa, nigra, cordata, incisia, amphicarpa* and *pilosa.* All these subspecies are found in the Mediterranean and the Near East, extending up to southern and central Europe. Other useful *Vicia* species include *V. ervilia* or bitter vetch, with its primary center in the Mediterranean. It was known to be cultivated for food in Turkey (7750 BP) and Greece (7500 BP). *Vicia narbonensis* or the narbonne vetch has its primary center of origin in eastern Georgia and a secondary center of origin in the Mediterranean. Narbonne vetch occurs as a weed in barley and wheat fields in Transcaucasia as does *V. villosa* or hairy vetch which is found in central Europe, the Mediterranean region and West Asia.

Vicia faba (Leguminosae) or faba bean probably originated in Southwest Asia or the Mediterranean. Its wild progenitor has not been identified with certainty although several theories have been put forward but discounted for one reason or another. A center of diversity has been established in the Mediterranean region. Several finds of the small-seeded var. *minuta* have been found in the archaeological remains. The oldest documented record of an archaeological find of large-seeded faba bean comes from Iraq around 1000 AD which perhaps accounts for the late development of the large-seeded types we see today.

Linum usitatissimum (Linaceae) or flax (linseed) was probably domesticated almost around the same time (ca. 8200 BP) as wheat and barley in the Near East from where it spread to other parts of the Old World along trade routes. Its wild progenitor, *L. bienne,* does not occur in Central Asia which Vavilov thought to be a center of origin of flax. *Linum bienne* has two main races: a continental winter annual found in the semi-arid foothills of Iraqi Kurdistan and Iran, and an Atlantic-Mediterranean form found along the coastlines. The latter is a perennial also sometimes referred to as *L. angustifolium.* It has a very high oil content. Hence, during the domestication process, according to some authors, two forms emerged, one for fibre (flax) and another for its oil (linseed).

Gossypium herbaceum (Malvaceae) or short-staple cotton, a native of southern Africa (see Holubec, this volume), was probably introduced to Ethiopia and thence to Arabia and Balochistan. It is widely cultivated in Syria and Egypt. In Iran it evolved into a special race which spread to western India where it was the first cotton to be cultivated. However, owing to its short staple it was not much in demand compared with the Egyptian cotton *G. barbadense* which is also later in maturity. Another cotton species, *G. incanum* or hillcoat cotton, became established in the Yemen, no doubt having arrived there from Ethiopia. It is extremely drought resistant as is *G. areysianum* found in southern Arabia. Another theory suggests that the northwestern part of the Indian subcontinent was probably the cradle of cotton cultivation, from which an 'ennobled' plant diffused to other parts of Asia Minor, the Near East, Africa and Europe. The earliest archaeological finds of cotton are from Mohenjo-Daro in the Indus Valley 2300 BC (Watson 1983).

Cannabis sativa (Moraceae) or hemp originated perhaps near the Caspian Sea. The first use of this plant was for fibre. Hemp is reckoned to be one of the oldest cultivated non-food crops. Evidence of the use of hemp in China goes back to Neolithic times. The crop reached West Asia around 2000 BC and was taken to Europe around 1500 BC. It became well established in the Mediterranean region.

Ficus carica (Moraceae) or common fig, one of the most ancient fruits of the Near East, arrived there from South East Asia, probably along the trade routes. However, it developed a secondary center in the Mediterranean and Asia Minor. By 6000 BP figs were cultivated in Egypt. It also grows wild in these regions and all over tropical Asia.

Nelumbo nucifer (Nelumbonaceae) or the Indian lotus is not native to India but to wetlands of northern Iran. It spread to China, Japan and India where it is often cultivated for its rhizomes and fruits. It was also grown for some time in the eastern Mediterranean region but is not found there today.

Olea europaea (Oleaceae) or olive is one of the longest-living fruit-bearing trees in the world (see Besnard *et al.,* this volume). It is one of the relics of an age when the Mediterranean had a somewhat tropical climate, i.e. during the mid-Tertiary period. Excavations in Palestine and elsewhere in the Mediterranean indicate that it is closely associated with the history of civilization, being the source of edible fruits and oil for over 10,000 years. There is little doubt that the olive tree was first domesticated in the eastern Mediterranean where wild *Olea europeae* subsp. *oleaster* forms thrive (Damania 1995). The Phoenicians, from such ancient cities as Ugarit on the Syrian coast, introduced the olive around 5000 BP to the west and a secondary center of diversity developed in the areas bordering the Aegean Sea. From there the tree spread to southern Italy and as far as Spain where groves known to be 1000 years old still exist.

Phoenix dactylifera (Palmae) or date palm is another tree plant whose cultivation goes back to ancient times in the Near East. This tree and its symbol are synonymous with Arabia. Its present natural distribution includes North Africa, the Middle East and the western coast of India. At one time in the past the genus *Phoenix* was widespread in Europe but retreated southward as the climate changed. Its cultivation goes back to Neolithic times. The earliest archaeological record dates back to 6500 BP from Egypt. Traces of date palm stones from 5000 BP have been found at achaeological sites in western India. Its wild ancestor is not known although it crosses readily with the two other species of palms - *P. dactylifera* and *P. reclinata. Phoenix atlantica,* or false date palm, could also be an ancestor or an intermediate form. *Phoenix atlantica* var. *maroccana* also produces edible fruits.

Papaver somniferum (Papaveraceae) or opium poppy is a native of West Asia. It is the source of opium which is obtained from dried latex which drips from cuts made in the unripe capsular fruits. *Papaver setigerum,* the wild progenitor, is found from Persia to the Balkans. Arab traders are credited with spreading the narcotic use of opium. The plant had reached China by the 18th century and was the principal cause of the Opium Wars.

Fagopyrum esculentum (Polygonaceae) or buckwheat was introduced into China, Tibet and northern India from Central Asia. It is cultivated as a grain crop and is highly nutritious. It is a popular food in Japan.

Rheum rhaponticum (Polygonaceae) or rhubarb of Europe and North America originates from Armenia and Azerbaijan around the Caspian Sea where several other species of *Rheum* are grown. In China and Tibet *R. palmatum* and *R. officinale* have been used in traditional medicine as laxatives since 2700 BC.

Punica granatum (Punicaceae) or pomegranate is the traditional fruit of the central Iranian plateau. It is also one of the most ancient fruit trees to be domesticated and is known to have been grown in the Hanging Gardens of Babylon. It has some cultural significance as well and is found in the central courtyard of every home in the central Iranian plateau. The field genebank maintained by the Agricultural Research Center at Yazd in central Iran has over 700 different types, some of which go back to antiquity (Damania *et al.* 1993). Its only related species is *P. protopunica* which is endemic to the island of Socotra (Yemen) in the Indian Ocean.

Cydonia oblonga (Rosaceae) or quince is native to southern Daghestan and Azerbaijan. It is cultivated in the Near East as a garden tree. Its fruits are used to make jam.

Malus pumila (Rosaceae) or apple and *Pyrus communis* (Rosaceae) or pear have their primary center of origin in Asia Minor, the Caucasus and Central Asia. The secondary centers of origin are more toward the east, perhaps in western China. However, both apples and pears have existed in Europe from prehistoric times.

Prunus armeniaca (Rosaceae) or apricot was thought by Vavilov to have its secondary center of diversity in the Near East. It is believed to be native to western China.

Prunus amygdalus, syn. *Amygdalus communis* (Rosaceae) or almond, has its primary gene center in Central Asia as well as the Near East region and is a fruit species of great antiquity. Syria has several cultivars. *Amygdalus fenzliana* or fenzel almond is found in Anatolia and is grown as an ornamental. *Amygdalus persica* or peach has its center of origin in China but also a secondary center in Afghanistan and northeastern Iran. The landraces in the native habitats have better taste but also have some bitter forms and are not uniform in shape and size and hence not preferred by commerce.

Prunus avium (Rosaceae) or sweet cherry comes from Asia Minor and wild trees can be found in West Asia and North Africa. Domestication is said to have occurred in different places, leading to several ecotypes. It is interesting to observe that the sweet forms were domesticated whereas the bitter ones were left to grow unprotected in the wild. Another *Prunus* spp. native to the Near East is *P. cerasifera* or cherry plum which grows wild in Caucasia, Iran, Asia Minor, the Altai and Central Asia. It could be one of the parents of *P. domestica* or the garden plum. *Prunus spinosa* or blackthorn or sloe is found all over the Near East, North Africa and the southern Mediterranean.

Pyrus spp. (Rosaceae) or pears. The Near East is the main geographic center of origin for this genus. *Pyrus caucasica, P. syriaca* and *P. takhtadzhiana* are some of the other species of *Pyrus* found in this region. Hybridization among the wild species is common and the progenies are appreciated as ornamentals, rootstocks for cultivated species, and increasingly in recent years as donors of genes of disease resistance in fruit-breeding programs, particularly in California.

Coffea arabica (Rubiaceae) or Arabic coffee has its primary center in southwest Ethiopia, where it was chewed before being used for making a beverage. From Ethiopia it migrated to the Yemen. The discovery that coffee could be brewed into a beverage was made in Arabia around the 15th century. A single coffee plant shipped by Dutch plant explorers to Amsterdam from the East Indies in 1706 was nurtured in the botanical garden of that city. Amsterdam was one of the major world centers of maritime trade in those days. Some of the seedlings from this single plant were taken via France to the Caribbean island of Martinique and from there to South America. Hence the genetic base of the Latin American coffee is indeed very narrow and devastating attacks of diseases are common. The African form *C. canephora* often provides genes for disease resistance. Besides Latin America, coffee is also cultivated in Kenya, India, Java and other parts of the East Indies. Coffee is said to be the second most valuable commodity in world trade after petroleum products.

Citrus medica (Rutaceae) or citron is probably the only citrus native to West Asia, although the northeastern part of India (Assam and the Indo-Burma border area) has been mentioned as a center of origin of citrus species. *Citrus medica* var. *ethrog* is used by people of the Jewish faith at the Feast of Tabernacles. Citron was grown in Sardinia and the area around Naples after the 3rd century AD.

Cuminum cyminum (Umbelliferae) or cumin is a native of the Levant whose fruits are used as spice in cooking, for flavoring soups, and are an essential ingredient of curries. Its essential oil is also used in perfumery. It is also grown extensively in the drier parts of western India.

Daucus carota (Umbelliferae) or carrot. Wild forms occur in West and Central Asia. However, a secondary center of diversity has developed in Turkey and unique landraces can even be found in Syria. There is evidence to believe that the carrot was domesticated in Afghanistan from where it spread all over the world, introgressing with the indigenous wild forms to give rise to local cultivars. Two main groups have been recognized: the Asian group with purple and yellow roots, and the Western group with mainly orange roots. In Turkey the two groups seem to converge and give rise to hybrids. In the Near East countries uniform non-hairy hybrid varieties from the West have become popular, but the natives still prefer the hairy purple type with non-uniform roots.

Foeniculum vulgare (Umbelliferae) or fennel is native to the Mediterranean where it has been cultivated since early times. All parts of the plant are aromatic. The essential oil is used as a flavoring agent.

Pastinaca sativa (Umbelliferae) or parsnip is a native biennial of West Asia and has been consumed as a root vegetable since Greek times. Feral forms are known with tough, dry roots. In the tropics, where it has not gained much popularity, parsnip grows well only at higher altitudes.

Pimpinella anisum (Umbelliferae) or anise was domesticated in the Orient and cultivated in the Near East for its aromatic fruits which are used to flavor strong liqueurs, such as Syrian 'arak' and the Greek 'ouzo'. It was known to the ancient Egyptians, Hebrews, Greeks and Romans and was valuable for medicinal purposes during the Middle Ages.

Celtis australis (syn. *C. excelsa*) (Ulmaceae) or hackberry is native to the eastern Mediterranean and one of the tree species whose fruits were gathered by early farmers from ancient times. The tree is cultivated as an ornamental and for its edible fruits (Mansfield 1959). Charred remains of fruits were found at the PPNB site of Nevali Çori, near Urfa, in southeastern Turkey in 1991 (see Pasternak, this volume).

Vitis vinifera (Vitidaceae) or grapevine is perhaps as old as time itself and was one of the first fruits to be domesticated from the wild in Central Asia, the Near East and the Mediterranean region. The wild progenitor, subsp. *sylvestris,* is found in areas bordering the Mediterranean Sea except in Libya and Egypt. Its primary center is probably in Armenia and northern Iran. Natural hybrids between the wild and cultivated forms are often found in Tajikstan and as a result newer cultivars come into existence all the time.

Conclusion

There is little doubt that the Near East and the Mediterranean regions have played a major role in the domestication and spread of several major and many more minor crops throughout the world. But why is it that crops originating in the Americas and Africa took a long time to spread to the rest of the world whereas crops domesticated in the region in and around the Fertile Crescent quickly spread far and wide? Most of the progenitors of 'founder crops' were not domesticated again elsewhere after their initial domestication in the Fertile Crescent. One of the explanations could be that the spread of domesticated crop plants was so rapid that people soon stopped gathering the wild species and began to eat only the cultivated crops. Eurasia's west-east axis permitted the Near East crops to promote agriculture over the band of temperate latitudes from Europe to the Indus Valley.

Another question which needs an answer is why the region which gave the world agriculture and several major crops finds itself today in the grip of food deficit? Some say that despite the early lead of the Fertile Crescent in agricultural development the region lost out eventually because of the ecologically suicidal and unsustainable policies adopted by the people of that region, e.g. deforestation, overgrazing, monoculture and the practice of irrigation without crop rotation. These practices destroyed the topsoil and caused widespread erosion as well as salinization followed by a drop in soil fertility and crop yields.

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The Spread of Neolithic Agriculture from the Levant to Western Central Asia - D.R. Harris

Introduction

For a symposium which brought together botanists and archaeologists to discuss recent research on the origins of agriculture in the Near East, it is fitting first to recall the profound influence on the subject of two early 20th-century pioneers, one a botanist, N.I. Vavilov, and the other an archaeologist, V. Gordon Childe.

It was in 1926 that Vavilov first portrayed in map form his concept of centers of origin of cultivated plants (Harris 1990). These he argued were to be found in "mountainous districts", which were not only the homelands of cultivated plants but also of "primeval agriculture" (Vavilov 1926:219). Southwest Asia, which he defined as stretching from the eastern Mediterranean to northern India, was the first of the five centers he proposed at that time, and the one where many of the Old World cereal and pulse crops had been domesticated.

Two years later Childe referred to Vavilov's work when he first adumbrated his hypothesis of the Neolithic or Agricultural Revolution, which proposed that animals were domesticated and agriculture began in the Near East (including the Nile Valley in Egypt) when the climate became more arid following the end of the last glacial period (Childe 1928:42-43). He subsequently elaborated this model, first briefly (Childe 1934:23-30) and then more comprehensively (Childe 1936:66-104), and it subsequently became widely known as Childe's 'desiccation', 'oasis' or 'propinquity' theory. Childe envisaged people and animals being forced by increasing post-glacial aridity (desiccation) into closer proximity (propinquity) around diminishing sources of water (oases) where sheep, goats and cattle were domesticated, a process that, he speculated, would have been facilitated if the people were already cultivating grain and the animals were attracted to the farmers' fields. In fact, he suggested that cereal cultivation (which he thought might have begun in Palestine or Egypt) preceded livestock-raising - a view that finds support today (see below). Vavilov (1926:244) was more concerned to show how a "thorough knowledge of cultivated plants, with their multitude of varieties and differentiation into geographical groups,... makes us refer [their] origin... to the remotest past" than he was to speculate about the particular environmental and cultural contexts of the earliest shifts to cultivation and domestication. Nevertheless, both men regarded the Near East as the region in which agriculture first originated, and their very different but parallel contributions to the subject encouraged later scholars, notably the American archaeologist Robert Braidwood (1960), to undertake archaeological field research on 'agricultural origins' in the region.

Since Vavilov and Childe laid the foundations of the subject in this way, new techniques of bioarchaeological research have been developed and much new evidence has been acquired in the field and laboratory. These investigations have tended to reinforce the view that the transition from hunting and gathering to agriculture took place earlier in Southwest Asia than elsewhere in the world, and that an exceptionally large array of plants and animals was domesticated in the region in the course of the transition. In this contribution to the symposium, attention is focused, however, not on the earliest stages of the process, but on the way in which the system of agropastoral production which originated in western Southwest Asia (the Levant) appears to have spread from that 'core area' during Neolithic times. In particular, the putative spread of agropastoralism northeast into Central Asia is examined in the light of new evidence from recent archaeological investigations in southern Turkmenistan. But before that topic is addressed directly, it is necessary to outline the temporal and methodological context of the study.

Chronology and methodology

The chronological context is the Neolithic which, in the southern and central Levant at least, is conventionally divided into two phases, the second approximately twice as long as the first, i.e. the Pre-Pottery (or Aceramic) Neolithic A (PPNA) from ca. 8500 to ca. 7500 bc, and the Pre-Pottery Neolithic B (PPNB) from ca. 7500 to ca. 5500 bc. (In this paper "bc" refers to uncalibrated radiocarbon dates, "BC" to calibrated dates). The PPNB is commonly subdivided into Early (ca. 7500-7200 bc), Middle (ca. 7200-6500 bc), Late (ca. 6500-6000 bc) and Final (alternatively called PPNC or even Early Late Neolithic, ca. 6000-5500 bc). Following the widespread

archaeological appearance of pottery by about 5500 bc, the PPNB is succeeded by the Pottery (or Ceramic) Neolithic (ca. 5500-4200 bc). An alternative chronological scheme (Cauvin 1987), not followed here, defines a sequence of Stages for the northern Levant, in which Stage 2 broadly corresponds to the PPNA, Stage 3 to the Early and Middle PPNB, Stage 4 to the Late PPNB and Stage 5 to the Final PPNB.

Although these chronologies, which are based on radiocarbon (^{14}C) dates, refer strictly to the southern/central and northern Levant respectively, they correspond sufficiently closely to each other, and refer to a sufficiently large region (the western Fertile Crescent), to provide a sound temporal framework for discussion of the origins and spread of agriculture in Southwest Asia as a whole. However, not all ^{14}C dates from archaeological sites and sequences are equally reliable because of sampling biases, unclear contextual associations, differences in materials sampled, and interlaboratory inconsistencies in sample-processing (Kuijt and Bar-Yosef 1994). We must therefore be both cautious and critical when comparing ^{14}C dates from different sites and constructing regional chronologies.

The data and methods of analysis on which the interpretation offered in this paper is based derive from four main fields of study: (1) the biogeography of the wild progenitors of the crops and domestic animals of Neolithic agropastoralism, (2) the bioarchaeology of plant and animal remains recovered from Neolithic sites, (3) analysis of the distributional, architectural and artefactual features of Neolithic settlements, and (4) the ^{14}C dating of Neolithic sites and sequences, including in particular the use of the accelerator mass spectrometric (AMS) ^{14}C technique to date individual seeds and bones from the Neolithic crops and domestic animals. These four sources of evidence are invoked in the discussion that follows, which starts by examining how the agropastoral system arose in the Levant and began to spread within the Fertile Crescent during the PPNA and the Early and Middle PPNB.

Origins in the Levant

Because this paper focuses on the Neolithic spread of agriculture and pastoralism, after the crops and livestock of the agropastoral system had been domesticated, we are not directly concerned here with the earlier stages of the transition from hunting and gathering, nor with the problematic question of how to define, and recognize archaeologically, the very beginnings of the process (see Harris 1998 for discussion of that currently controversial question). For our purposes, it is sufficient to start at a point along the continuum of interaction between people, plants and animals where agriculture and pastoralism, based on crop cultivation and the raising of domesticated animals, are being practised, in contrast to techniques of wild plant and animal management (cf. Harris 1996a:444-456).

Leaving aside the question of how plants and animals were exploited by the immediately pre-Neolithic (Epipalaeolithic) people of the Levant, we can start by recognizing, from the bioarchaeological evidence, the presence in the PPNA and Early and Middle PPNB of a suite of domesticated cereals, pulses and one oil/fibre crop - barley, einkorn and emmer wheat, pea, lentil, chickpea, bitter vetch and flax - which constitute the 'founder' crops of Southwest Asian agriculture (Zohary 1989, 1996; Zohary and Hopf 1993). Table 1 gives the full nomenclature of these crops and of their wild progenitors, and Fig. 1 shows the location of the archaeological sites from which their remains have been recovered.

As Fig. 1 shows, only three PPNA sites, all in the southern and central Levant (Jericho, Iraq el-Dubb and Aswad I), have yielded remains of (cereal) crops interpreted as domestic. The crops are two-row barley, emmer and einkorn. Remains of lentils and other herbaceous legumes also have been recovered, but whether they are from wild or domestic forms cannot be determined because of their charred state. The primary evidence for the presence of domesticated cereals and other possible crops at the three sites in the PPNA is presented in Hopf (1983:591-592, 605, 609, 611), Colledge (1994:163-165, Table 5.4) and van Zeist and Bakker-Heeres (1982:171,185-190). In the southern Levant, along the middle Euphrates and in the catchment of the upper Tigris, there are six other PPNA sites where remains of morphologically wild forms of barley, einkorn, rye, lentil, pea and bitter vetch have been found (Fig. 1). As a group, all the PPNA sites are located within areas in which the wild progenitors of barley, einkorn, emmer, pea, lentil, bitter vetch and flax occur today and are believed to have done so in early Neolithic times, although the wild ancestor of the chickpea is restricted today to southeastern Turkey (Zohary 1989). From the presently available archaeobotanical evidence of the plant remains, coupled with the data on the ranges of their wild progenitors, we can infer that during the PPNA the wild cereals and pulses were widely harvested, and perhaps cultivated, by hunter-gatherer groups in the western Fertile Crescent and that the cereals (at least) may possibly have been domesticated first in the central and/or southern Levant.

Table 1. The 'founder' crops of Southwest Asian agriculture.

English name		Traditional binomial[†] and authority of cultivated crop	Traditional binomial and authority of wild progenitor
Barley		*Hordeum vulgare* L.	*Hordeum spontaneum* C. Koch
	Two-row	*H. vulgare* subsp. *disticum*	
	Six-row	*H. vulgare* subsp. *vulgare*	
Einkorn wheat		*Triticum monococcum* L.	*Triticum boeoticum* Boiss. emend. Schiem.
Emmer wheat		*Triticum dicoccum* Schübl.	*Triticum dicoccoides* (Körn.) Aarons.
Lentil		*Lens culinaris* Medik.	*Lens orientalis* (Boiss.) Hand-Mazz.
Pea		*Pisum sativum* L.	*Pisum humile* Boiss. & Noë
Chickpea		*Cicer arietinum* L.	*Cicer reticulatum* Ladiz.
Bitter vetch		*Vicia ervilia* (L.) Willd.	Never named as an independent species
Flax		*Linum usitatissimum* L.	*Linum bienne* Mill.

Sources: Zohary 1989:371; Zohary and Hopf 1993:24, 58, 88, 95-96, 102, 110, 120.

[†] The traditional binomials are given here because they are still widely used by archaeobotanists, but, strictly, the rules of nomenclature require that the wild progenitors be named as subspecies (wild races) of the crops, e.g. wild barley should be referred to as *Hordeum vulgare* subsp. *spontaneum.*

Fig. 1. The Fertile Crescent and Anatolia: distribution of Pre-Pottery Neolithic A (PPNA: ca. 8500-7500 bc) and Pre-Pottery Neolithic B (PPNB: ca. 7500-6500 bc) sites from which remains of the founder crops of Southwest Asian agriculture have been recovered; data from Garrard (1996) and Zohary and Hopf (1993). Sites (PPNA (in bold), PPNB)

1: Beidha; 2: Nahal Hemar; 3: Jilat 7; 4: **Jericho,** Jericho (Tell es-Sultan); 5: **Netiv Hagdud;** 6: Ain Ghazal; 7: **Iraq el-Dubb;** 8: Yiftah-el; 9: **Aswad I,** Aswad II; 10: Ghoraifé I; 11: **Mureybit II, III;** 12: **Jerf el-Ahmar;** 13: Halula; 14: Can Hassan III; 15: Haçilar; 16: Asikli Höyük; 17: Cafer Höyük; 18: Çayönü; 19: **Hallan Çemi;** 20: **Quermez Dere**; 21: **M'lefaat**; 22: Ganj Dareh; 23: Abdul Hosein; 24: Ali Kosh.

There is no conclusive evidence for the presence of the 'founder' domestic animals of Neolithic agropastoralism - goats and sheep - at PPNA sites, and it is likely that agriculture in the Levant was initially based on cereal (and probably pulse) cultivation, with agropastoralism only developing later, during the Middle PPNB (see below).

Although wild, and possibly domesticated, cereals and pulses are likely to have been cultivated in the Levant during the PPNA, it is probable that this was a minor subsistence activity carried out in the vicinity of the typically small but permanent settlements, probably on patches of alluvium with water-retentive soils. There is abundant bioarchaeological evidence that the inhabitants of these sites hunted, trapped, fished and gathered a wide variety of wild animals and plants (Clutton-Brock 1978; van Zeist and Bakker-Heeres 1982; Hillman *et al.* 1989; Kislev 1989; Bar-Yosef and Belfer-Cohen 1991; Tchernov 1995). Thus an essentially foraging economy, with a minor component of crop cultivation, characterized the PPNA. It was not until after ca. 7500 bc, during the PPNB, that agriculture and pastoralism became the dominant modes of subsistence for a majority of the population of Neolithic Southwest Asia.

The establishment of agropastoralism in Southwest Asia

Evidence for the widespread development of an agropastoral economy during the two millennia of the PPNB comes mainly from changes in the distribution, size and architecture of settlements and from increases in the diversity and relative abundance of the remains of crops and domestic animals found at the sites. Comparison with the PPNA settlement pattern shows a substantial increase in the number of sites and an extension of their overall distribution beyond the Levant and the northern margins of the Fertile Crescent northwest into south-central Anatolia and southeast along the foothills of the Zagros Mountains. The increased number of settlements was accompanied by increases in their size, particularly in the Levant and southeastern Anatolia. These changes increased dependence, at least in the larger 'villages', on local agricultural production and a corresponding decrease over time in dependence for food on wild plants and animals. Architectural changes also occur in the PPNB, notably from the curvilinear structures characteristic of earlier periods to rectilinear layouts of rectangular, mainly mud brick houses with features such as internal fireplaces or ovens, containers for storage, and plaster floors.

When these changes in settlement pattern and architectural style are viewed in conjunction with the more

abundant evidence at the PPNB sites for crops and domestic animals, it becomes clear that we are witnessing the establishment and spread within Southwest Asia of an essentially new way of life based increasingly on agriculture and pastoralism, and involving the elaboration of exchange networks which connected the growing settlements and promoted the diffusion of ideas and techniques as well as products.

Comparison between the PPNA and Early and Middle PPNB shows that a major change took place over that time period. Compared with only three PPNA sites, in the southern and central Levant, which have yielded possible evidence of domesticated crops, there are, by the Middle PPNB, 17 sites with definite evidence of such crops, and they are distributed across most of the Fertile Crescent and west as far as central Anatolia (Fig. 1). The representation of the founder crops also increases to include - in addition to two-row barley, einkorn and emmer - naked six-row barley, free-threshing (tetraploid and hexaploid) bread and hard wheat, and rye; and the pulses, especially lentil and pea, are now more widely represented (Garrard 1996), although discrimination between wild and domestic forms remains problematic.

Although this bioarchaeological record of the founder crops is still quite meagre and is hampered by problems of identification and of intersite variations in recovery techniques, the evidence for domestic goats and sheep is even more inadequate (Bar-Yosef and Meadow 1995:82-90; Legge 1996). But, taken as a whole, the evidence for the appearance of domestic caprines in Southwest Asia suggests that they may have been present at a very few Levantine sites (Abu Hureyra, Aswad, Jericho) before the beginning of the Middle PPNB (ca. 7200 bc), and that size reduction (which is an indicator of domestication) began later in sheep than in goats, perhaps not until the end of the Middle PPNB (ca. 6500 bc) in the Levant (Bar-Yosef and Meadow 1995:89). There, up to a millennium apparently separated the beginnings of cereal cultivation and of caprine husbandry. However, by the end of the Final PPNB (ca. 5500 bc) domestic goats and sheep are found at Neolithic sites throughout Southwest Asia, frequently associated with evidence of cereals. It is, therefore, in the later Middle PPNB and especially the Late PPNB, i.e. during the 7th millennium, that we can expect agropastoralism to have become the dominant mode of subsistence across much of the region.

Despite recent advances in archaeological and biological research on the earliest crops and domestic animals, the bioarchaeological evidence is still too uneven and uncertain to permit well-grounded hypotheses about precisely where within Southwest Asia the cereals, pulses and caprines were first domesticated. However, regardless of these uncertainties, we can confidently hypothesize that agropastoralism, as a functionally integrated system of crop and livestock production, came into being during the PPNB, probably no earlier than the Middle PPNB, and that by the end of the PPNB villages sustained mainly by a combination of grain (cereal and pulse) cultivation and (sheep and goats) herding were established throughout the Fertile Crescent from the southern Levant to the central Zagros.

Whether the spread of agropastoralism was due more to adoption of this new way of life by pre-existing hunter-gatherer groups or to colonization by farmers remains uncertain. But it can be argued that the functional integration of grain and livestock production in a system of mixed farming - in which cereals and pulses were grown on the flatter, better-watered, mainly lowland soils and sheep and goats grazed and browsed on rougher upland terrain (whether locally or by means of seasonal transhumance) - proved to be highly effective, ecologically and nutritionally, in sustaining the growing number of sedentary villages. The grain crops alone provided a mix of carbohydrates, vegetable proteins and oils which contained most of the essential nutrients, and this was augmented by animal protein and fat from the caprines. An assured supply of new weaning foods derived from the cultivated cereals - with the addition of milk after goats and sheep began to be routinely milked, perhaps not until after the PPNB - as well as increased storage of grain in the villages and of animal products 'on the hoof, would also have tended to accentuate population growth and stimulate the foundation of new settlements near cultivable land, thus promoting agricultural colonization. Agropastoralism can therefore be seen as a uniquely successful self-sustaining subsistence system which had a 'built-in' tendency to expand spatially and was not restricted territorially by a need for continued access to wild plant and animal foods, as were the hunter-gatherer subsistence systems that it progressively replaced.

By the end of the PPNB agropastoralism had come to support most of the inhabitants of the Fertile Crescent and had spread northwest across Anatolia and southeast to the southern Zagros. Bar-Yosef and Meadow (1995:Fig. 3.6) have constructed the extent of this spread and they also indicate by arrows the directions of further expansion northwest into Europe, southwest to the Nile Valley, southeast toward the Indus Valley and northeast to Central Asia. It is to the last of these putative expansions beyond the Fertile Crescent that we now turn our attention.

The development of agropastoralism in western Central Asia

The next logical step in attempting to trace the postulated spread of agropastoralism toward Central Asia would be to examine the archaeological evidence of Neolithic settlements associated with the remains of crops and domestic livestock in the western half of the Iranian Plateau, east of the crest of the Zagros Mountains.

Unfortunately, however, this vast area of mountains, upland valleys, steppe and desert is almost devoid of excavated Neolithic sites, the main exception being Tepe Sialk (Fig. 2), near the modern town of Kashan, where the Pottery Neolithic is represented in the lowest levels (Ghirshman 1938-39:74-77). Remains of domestic two-row hulled barley and of domestic goats were found in these levels (Sialk I), as well as stone hoe and sickle blades, suggesting that agropastoralism was practised at Sialk from the time the site was first occupied, which may have been ca. 5500 bc (Mellaart 1975:187-188). Excavations at another Neolithic tell - Tepe Zaghe - northwest of Sialk and about 65 km south of the town of Qazvin, have revealed early ceramic, and even some aceramic, levels, associated with small rectangular mud brick houses with plastered platforms, dated (by one ^{14}C determination) to 6269±150 bc (Neghaban 1971; Mellaart 1975:190, 194), which suggests initial occupation there in the Late PPNB.

Farther east, along the northern margins of the Iranian Plateau and the southern shores of the Caspian Sea, there are no reported Neolithic sites until the Elburz Mountains are reached, where there is a tell site, Tepe Hissar, on the southern slopes of the mountains near Damghan, and, still farther east, three sites in the Gorgan Valley (Tureng, Shir-i Shayn and Yarim) and another cluster of small tells (at Sang-i Chakmak) near the town of Bastam (Fig. 2). It is not until one reaches the piedmont zone of southern Turkmenistan, between the northern edge of the Iranian Plateau (formed by the Kopet Dag Range) and the Kara Kum Desert to the north, that known Neolithic sites become more numerous. Several of them have been excavated since the 1950s, and the existence recognized of a local Pottery Neolithic 'Jeitun Culture' (Masson 1957, 1961, 1971; Masson and Sarianidi 1972:33-46; Mellaart 1975:209-216; Kohl 1984:45-55). Recent investigations by an international team of British, Russian and Turkmenian archaeologists have sought to determine how agriculture began in the piedmont zone and have included further excavations at the eponymous site of Jeitun (Masson 1992; Harris *et al.* 1993, 1996; Harris and Gosden 1996). In view of the dearth of information on Neolithic settlement on the Iranian Plateau, we can best approach the questions of whether, and if so how, when and by what route agropastoralism spread from the Fertile Crescent to western Central Asia, by examining the evidence now available from southern Turkmenistan.

Fig. 2. The northern Iranian Plateau and Kopet Dag Piedmont: Pottery Neolithic sites and present-day zone of dry-summer tropical (mediterranean) climate; site distribution after Kohl 1984, Mellaart 1975 and Sarianidi 1992, climatic zone modified from Trewartha 1960. Sites (Mesolithic (in bold), Pottery Neolithic)

> 1: Zaghe; 2: Sialk; 3: Hissar; 4: **Ghar-i Kamarband**; 5: **Hotu**; 6: **Ali Tappeh**; 7: Sang- i-Chakmak;
> 8: Shir-i Shayn; 9: Tureng; 10: Yarim; 11: **Jebel**; 12: **Dam Dam Cheshme**; 13: Naiza; 14: Bami; 15:
> Kelyat; 16: Gievdzhik; 17: Pessedjik; 18: Togolok; 19: Chopan; 20: New Nissa; 21: Jeitun; 22: Yarti
> Gumbez; 23: Mondjukli; 24: Gadimi; 25: Chagylly.

Survey and excavation of Jeitun Culture sites in the western half and at the eastern end of the Kopet Dag piedmont by Soviet archaeologists in the 1950s and 1960s established a regional Neolithic sequence divided into three ceramically defined phases; and evidence of animal bones and impressions of barley and wheat grains in the mud bricks used to construct the settlements demonstrated that the inhabitants cultivated cereals, raised domestic goats and sheep, and hunted gazelle and other wild mammals. Only two of the sites were ^{14}C dated: Togolok, on the western piedmont, where Middle Jeitun levels were dated to 5370±100 bc (Mellaart 1975:212), and Chagylly, on the eastern piedmont, where Late Jeitun levels were dated to 5050±110 bc and grains of barley and wheat were also found (Masson and Sarianidi 1972:33, 42). No ^{14}C dates were obtained for the type site of Jeitun, which defined the Early Jeitun phase, but the excavator (Masson) suggested, because there were close similarities between its artefact, especially ceramic, assemblages and those from upper levels at the far-away sites of Jarmo and Tepe Guran in the Zagros, that Jeitun had been occupied in the 6th millennium (Masson and Sarianidi 1972:36, 171), an inference that has since been confirmed by a series of ^{14}C dates from the site (see below).

From 1989 to 1994 excavation at Jeitun was renewed and off-site ecological surveys were undertaken. A principal objective of these new investigations was to obtain from the site evidence of agriculture in the form of cereal or other plant remains and to date them directly by the AMS ^{14}C method. Systematic sampling and flotation were employed throughout the excavation of parts of the site (Harris *et al.* 1996:426-429) and our preliminary results confirm that barley and wheat were cultivated locally and sheep and goats raised. A suite of 11 AMS dates from the site, all from charred cereal remains, also confirms that agriculture was being practised at Jeitun by slightly before 5000 bc, or ca. 6000 BC calibrated (Harris *et al.* 1996:436).

The range of cereals so far identified is, however, less than at most Southwest Asian Neolithic sites. Domestic einkorn is present in all the samples analyzed, but (contrary to our earlier report, in Harris *et al.* 1993:332) none of the cereal remains can definitely be identified as from domestic emmer; both naked and hulled barley occur at low frequencies, but there is no evidence of any of the pulse crops (Charles and Bogaard 1996). Quite a wide

spectrum of wild and weedy herbaceous plants, including grasses, sedges, legumes and crucifers, has also been identified, and, when analyzed by time of flowering/fruiting can be classified into two groups: those that arrived on site as 'probably harvested' crop weeds and those that probably did so in sheep/goat dung. Analysis of the plant remains from Jeitun, coupled with confirmation from the new excavations of the abundance of sheep and goats (as well as gazelle), suggests that the inhabitants practised a form of agropastoralism essentially similar to that in evidence at Middle and Late PPNB sites in the Fertile Crescent. The apparent absence of emmer at Jeitun does, however, appear anomalous, particularly because it is usually more abundant than the other wheats, and sometimes barley, in the Neolithic crop assemblages of the Fertile Crescent. If its absence, and the dominance of einkorn, is confirmed by analysis of further samples from Jeitun, an explanation of this apparently anomalous situation may lie in selective adaptation to local conditions, which (despite average annual precipitation - today - being less than 250 mm) might have favored the cultivation of drought-tolerant forms of einkorn as a rain-fed winter cereal rather than the cultivation of typical forms of emmer, which in this environment would require irrigation. Another explanation of the anomaly could be that emmer was not introduced with einkorn as part of a Neolithic crop 'package' coming from farther west, a possibility that could best be tested by archaeobotanical work at other early Jeitun Culture sites on the piedmont.

Mention of the introduction of a Neolithic 'package' from the west brings us back to the main theme of this paper and raises the fundamental question of whether any of the founder species of Neolithic agropastoralism in Southwest Asia which have been identified at Jeitun, i.e. einkorn, ?emmer, barley, goats and sheep, could have been domesticated locally rather than introduced as domesticates. Reference has already been made to Zohary's (1989) account of the identification and distribution of the wild progenitors of the founder crops, which shows them to be largely concentrated in the Fertile Crescent, with some species extending westward and/or eastward, mainly as weedy forms. In the updated versions of his 1989 maps published with Hopf in 1993 there are only very minor changes in the distribution patterns, which still show that neither wild einkorn nor wild emmer occurs today east of the Zagros Mountains. Wild barley too occurs mainly in the Fertile Crescent, but "more isolated populations, usually of weedy forms" do extend east across Central Asia as far as Tibet (Zohary 1989:360). Valuable additional information on the present-day distribution of wild wheats and barley, incorporating new field data, is now available from the work of Jan Valkoun *et al.* (this volume). Although their map of the distribution of *Triticum boeoticum* (wild einkorn) marks a few collection sites farther east in Iran than any shown by Zohary and Hopf (1993:34), the sites are still confined to the mountains of western Iran (southern Zagros and western Elburz), and their map of the distribution of *T. dicoccoides* (wild emmer) does not extend its distribution eastward at all in comparison with Zohary's and Hopf's map (1993:41).

Assuming that the distributions of the wild progenitors did not differ grossly in Neolithic times from the present patterns, we can exclude the possibility of local domestication, east of the Caspian Sea in southern Turkmenistan, of both einkorn and emmer. Barley is more problematic, in that apparently wild stands of the wild progenitor occur in southeastern Turkmenistan and northeastern Iran today (Harris and Gosden 1996:386), but these populations have characteristics, such as an upright habit and synchronised tillering and seed maturation, which suggest that they are descended from weedy forms introduced with domestic barley during the spread of Neolithic agriculture from farther west (Jan Valkoun, pers. comm.). The probability is therefore that barley was not independently domesticated in western Central Asia and that the remains recovered at Jeitun and Chagylly derived from domestic barley originally introduced from Southwest Asia.

The natural ranges of the wild progenitors of domestic sheep and goats -respectively the western Asiatic mouflon (*Ovis orientalis* Gmelin) and the bezoar (*Capra aegagrus* Erxleben) - extend across Southwest Asia and into Central Asia (Harris 1962; Uerpmann 1987:113-118, 124-132, 1989), so their local domestication in southern Turkmenistan appears to be a possibility. But, although the bezoar is native to the area, the range of the Asiatic mouflon extends eastward only as far as the Elburz Mountains, where it overlaps the western limit of the urial (*Ovis vignei* Blyth) (Clutton-Brock 1981:53-54; Uerpmann 1987:126-130). The mouflon does not extend into Turkmenistan, and although the urial can interbreed with the mouflon - viable hybrids have been reported in north-central and southeastern Iran (Valdez *et al.* 1978; Meadow 1989:29) - it has a higher chromosome number than the mouflon and is unlikely to be a direct ancestor of domestic sheep (Clutton-Brock 1981:54).

Consideration of the distributions of the progenitors of the early Neolithic crops and domestic animals represented at Jeitun thus tends to support the view that they were introduced to the Kopet Dag piedmont rather than domesticated locally, although local domestication of the goat cannot be wholly excluded on these grounds. There is no evidence reported of domestic (or wild) cattle at Jeitun, but according to Masson and Sarianidi (1972:44) the "abundant osteological evidence from the upper [Late Jeitun] layers" at Chagylly "points to cattle... having been domesticated." Small numbers of wild boar bones have been recovered at Jeitun and they have been reported from other Jeitun Culture sites, but there is no indication at present that domestic pigs were part of the Neolithic economy.

Viewed overall, the bioarchaeological evidence from Jeitun and the other Jeitun Culture sites on the piedmont suggests the presence from ca. 5000 bc of an already 'developed' Neolithic agropastoral system which strongly

resembles the village-based grain-caprine economy of the PPNB in the Fertile Crescent. There are similarities too in settlement pattern, architecture and artefacts. The Jeitun Culture settlements were small, compact villages consisting of rectilinear mud brick structures, most of which were single-roomed houses with lime-plaster floors and interior ovens with adjoining low platforms (Masson and Sarianidi 1972: Fig. 9; Harris *et al.* 1996: Figs. 3-6). Clay figurines and 'gaming counters', pottery, small stone axes and an array of other tools are very similar to artefacts found at Neolithic settlements in the Fertile Crescent, particularly at such Zagros sites as Jarmo, Tepe Guran and Tepe Sarab (Masson and Sarianidi 1972:45).

The implication of these similarities is that the settlement-subsistence system of the Jeitun Culture is more likely to have been 'implanted' in the piedmont zone from outside than to have developed *in situ* from local pre-Neolithic precursors. This conclusion is reinforced by the fact that all the known Early Jeitun sites are located on the western piedmont whereas the eastern sites (insofar as they have been excavated) lack evidence of early occupation - implying that settlement spread eastward across the piedmont during the 6th millennium and that the antecedents of the Jeitun Culture are most likely to be found farther west in Turkmenistan or northeastern Iran.

This line of reasoning directs attention to the valleys of the Sumbar and Chandyr Rivers which dissect the western end of the Kopet Dag Range and give easy access to the piedmont zone from the west (Fig. 2). These long east-west trending valleys are well suited to rain-fed agriculture, having higher rainfall than the piedmont and deeper, more fertile soils, and they appear to offer likely routes for the spread of Neolithic agropastoralism into southern Turkmenistan. In 1995 this possibility was investigated by members of the international team who had worked at Jeitun. They found, and trial-excavated, eight rock shelters and one open site in the Sumbar and Chandyr Valleys but detected no signs of Neolithic (or earlier) occupation other than three pottery sherds of unknown type which may be Neolithic (Gosden *et al.* 1996). This surprisingly negative result does not of course mean that the valleys were not settled by Neolithic farmers - early sites may have been buried under more recent alluvium or destroyed by later agricultural activities - but it does show that it will not be easy to test the hypothesis that these upland valleys functioned as conduits for the spread of agropastoralism to the piedmont zone.

In searching for the antecedents of the Jeitun Culture, attention turns next to the few known Neolithic sites, already referred to, in the Gorgan Valley and on the southeastern side of the Elburz Mountains (Fig. 2). At Yarim and Tureng, pottery of Jeitun Culture type was recovered from the lowest occupation levels although at Tureng only Late Jeitun ceramics were found (Crawford 1963; Deshayes 1967; Sarianidi 1992:113). At Sang-i Chakmak (Sang-e Caxmaq) there are several small tells, two of which - the eastern and western tells - have been partially excavated (Masuda 1974a, 1974b, 1976). The architecture, pottery and other artefacts of the eastern tell closely resemble the material culture of the Jeitun sites as well as that found at Yarim, and although there are no ^{14}C dates from it, it is thought to date to the Late Jeitun phase. The western tell proved to be almost devoid of pottery, but architecturally it is very similar to the Jeitun sites (Aurenche 1985:236, Fig. 3). Two ^{14}C dates, of 5505±155 bc and 5540±130 bc, were obtained from the middle occupation levels, which, when calibrated and compared with the AMS dates from Jeitun, indicate that the western tell at Sang-i Chakmak was occupied some 200-300 years before Jeitun (Harris and Gosden 1996:382). This comparison suggests that the Sang-i Chakmak tells, and possibly those in the Gorgan Valley, may represent antecedents of the Jeitun Culture, but without more complete excavation and dating of them this possibility cannot be confirmed.

In seeking evidence for possible local antecedents of the Jeitun Culture we should consider, in addition to the Neolithic tells in northeastern Iran, the rock shelter sites with evidence of Mesolithic occupation that exist close to the southern and eastern coasts of the Caspian Sea (Fig. 2). They form two clusters: the south-Caspian sites of Ali Tappeh, Hotu and Ghar-i Kamarband (Belt Cave), which were investigated by Coon (1957) and McBurney (1968), and the east-Caspian sites of Jebel and Dam Dam Cheshme at the foot of the Bolshoi Balkhan Mountains, which were excavated by Okladnikov (1956) and Markov (1966). Gupta (1979:II:49-52) suggested, mainly on the grounds of the almost complete absence of pottery at the western Sang-i Chakmak tell and some similarities in the stone tools, that the site might represent a transition from the south-Caspian Mesolithic to the Jeitun Culture. It is quite possible that there were connections across the Elburz Mountains in the late Mesolithic/early Neolithic, but occupation had ceased at Ali Tappeh by ca. 9000 bc, and, although (?domestic) sheep and goats increase at the two other rock shelters after ca. 7500 bc and pottery appears by ca. 6100 bc shortly before these sites too are deserted (Mellaart 1975:209), the postulated cultural similarities with Sang-i Chakmak appear tenuous. It is more likely that such 'Neolithic' elements as are present in the south-Caspian sites, and the early Neolithic culture of Sang-i Chakmak, both derive from farther west (see below).

A somewhat different problem arises when we consider the east-Caspian sites. The rock shelters excavated here are thought to have been occupied from the 10th to the 5th millennia, and they yielded bones of domestic goats and sheep (as well as abundant gazelle, onager and fish bones) in levels dated to the 6th and early 5th millennia. No evidence of crops was reported, but the sites were excavated before modern techniques of recovery of very small plant (and animal) remains, e.g. by flotation, were generally applied. The potential significance of these long-occupied sites has led members of the international team that worked recently at Jeitun to initiate a program

of site survey and excavation in the hope of determining more precisely the nature of the local Mesolithic-Neolithic occupation and its possible relationship with the Jeitun Culture, but results are not yet available from the first field season in 1997, when limited excavation was carried out in several rock shelters, flotation was systematically applied and samples taken for AMS dating.

The presence of the remains of domestic caprines in the rock shelter deposits could be explained in several ways: that resident hunter-gatherers were herding caprines adopted from Jeitun Culture farmers, that they were hunting feral goats and sheep, or that transhumant pastoralists from the Jeitun Culture villages used the rock shelters seasonally. We hope to obtain new evidence that will help us choose between these hypotheses, and also demonstrate whether the occupants of the rock shelters cultivated any crops (or perhaps obtained grain from elsewhere). However, even in the absence of such new evidence it is highly improbable that the Jeitun Culture developed out of the east-Caspian Mesolithic, although the interesting question of how the inhabitants of the sites in the Bolshoi Balkhan region interacted with those living on the piedmont in the 6th millennium itself deserves investigation.

When we look still farther west, beyond the southeastern Caspian and the eastern Elburz Mountains, for similarities to and antecedents of the Jeitun Culture, we encounter the problem, already mentioned, of the lack of excavated Neolithic settlements on the Iranian Plateau. Over 600 km (in a direct line) of mountain and desert terrain separate the eastern-Elburz and Gorgan Valley sites from the easternmost Neolithic sites of the Zagros; and Sialk I, which Mellaart (1975:194) interprets as culturally equivalent to the Jeitun Culture and Masson and Sarianidi (1972:45) claim has 'as its basis, local Neolithic traditions of the Djeitun type', lies over 400 km southwest of Sang-i Chakmak across the forbidding desert of Dasht-e-Kavir. Even the closest sites with excavated Neolithic levels in northern Iran - Hissar and Zaghe - are over 300 km apart (Fig. 2), and it is difficult to infer anything about possible early Neolithic connections between them from the published reports (Schmidt 1937; Neghaban 1971).

In the absence of new archaeological investigations in northern Iran, we cannot at present follow a trail of Neolithic settlement westward, in the hope of tracing more precise connections between the PPNB and/or the early Pottery Neolithic of the eastern Fertile Crescent and the Pottery Neolithic Jeitun Culture sites. But we can, in conclusion, speculate about when and by what route agropastoralism spread from west to east, and ask whether colonization is likely to have been the dominant process or whether the spread was due more to pre-exisiting Mesolithic hunter-gatherers adopting grain cultivation and caprine herding.

Conclusion: the spread of agropastoralism from the Fertile Crescent to western Central Asia

We have already established that by the end of the PPNB, ca. 5500 bc, most of the inhabitants of the Fertile Crescent, from the southern Levant to the central Zagros, were supported by an agropastoral village-based economy, which, as an integrated system of grain cultivation and caprine herding, is unlikely to predate the beginning of the Middle PPNB, ca. 7200 bc. We also know that by 5000 bc a 'developed' Neolithic grain-caprine economy was in place, as the Jeitun Culture, on the Kopet Dag piedmont in southern Turkmenistan and probably a few centuries earlier at Sang-i Chakmak and other early Neolithic sites in northeastern Iran. The maximum time available for the spread of agropastoralism from the Fertile Crescent to the region of the Jeitun Culture is therefore about 2000 years, but a more realistic estimate, which spans the period between the Late PPNB in the Zagros (including the partly aceramic site of Tepe Zaghe already referred to) and the beginning of Jeitun settlement, is about 1000 years, i.e. from ca. 6300 to ca. 5300 bc.

Any attempt to infer the route by which agropastoralism spread must also be speculative, but here the assumption made is that it would have done so in the environment most favorable to rain-fed agriculture in the area between the Zagros and the Kopet Dag piedmont. This assumption is likely to be valid even if the Neolithic farmers were familiar with techniques of irrigation and added water to their fields to ensure or enhance grain production, because both rain-fed and irrigation agriculture would have been more dependable and productive in this zone than in any of the other major biomes of northern Iran: the high mountains, the deserts to the south, and the heavily forested coastal lowlands to the north. Allowance should be made for climatic and other environmental changes that may have occurred in the area during and since the 6th millennium (about which we are presently ignorant), but the contrasts in terrain between upland and lowland and between forest, steppe and desert are so extreme in northern Iran that any such changes are unlikely greatly to have altered the west-east trending pattern of climatic and vegetational zones.

Today the zone most propitious for agriculture is that designated by the so-called mediterranean or dry-summer subtropical climate with its associated woodland/grassland vegetation containing a great diversity of woody and herbaceous species growing on rocky slopes (well suited to caprine pastoralism) and on fertile valley soils (well suited to grain cultivation). This zone extends from the northeastern Fertile Crescent in a long narrow lobe that projects west-east south of the Caspian Sea to approximately 60 E longitude (Fig. 2). It encompasses the middle and lower elevations of the Elburz Mountains and the Gorgan Valley, and follows the course of the Atrek River

(including its north-bank tributaries the Sumbar and Chandyr) as far east as the modern city of Mashhad. It offers an inviting 'corridor' for the spread of agropastoralism from the northern Zagros to the Kopet Dag piedmont, and one where systematic prospecting for early Neolithic sites is likely to be rewarded.

Even if these speculations about when and by what route agropastoralism spread to western Central Asia are broadly correct, they leave open the question of whether it reached the Kopet Dag piedmont as a result mainly of colonization by farmers (primary or demic diffusion) or the adoption of domesticates and agropastoral techniques by resident foragers (secondary diffusion). These need not, of course, be mutually exclusive processes, and it is likely that both colonization and adoption occurred, but the conclusion to be drawn from the evidence and reasoning presented in this paper is that the spread of agropastoralism across northern Iran was due primarily to colonization. This conclusion is based partly on the (already discussed) assumption that the grain-livestock mixed-farming system which originated in the Fertile Crescent during the PPNB was inherently expansive and accentuated population growth; partly on the - admittedly still rather tenuous - evidence for similarities in the material culture of Neolithic sites in the eastern Fertile Crescent and the Jeitun Culture region; and partly on the fact that when the Jeitun Culture appears archaeologically at ca. 5000 bc it does so relatively suddenly and exhibits the main features of a 'developed' Neolithic economy in the Fertile Crescent: small village settlements with rectilinear mud brick architecture, pottery and domesticated barley, wheat, goats and sheep. However, this conclusion does not preclude the possibility that some of the elements of the agropastoral economy (e.g. goats, sheep, pottery) were selectively adopted through trade or by other means, such as intermarriage, by hunter-gatherer groups living in the region, e.g. at the rock shelter sites in the Bolshoi Balkhan Mountains.

If colonization from the west was responsible for the foundation of the first Jeitun Culture settlements it is likely to have taken place quite rapidly, spreading from the northern Zagros to the western Kopet Dag piedmont within a millennium. If, as is suggested, the spread took place along the zone of mediterranean climate across northern Iran the distance was of the order of 1000 km, thus suggesting an average rate of spread of approximately 1 km per year. Interestingly, this approximation is of the same order of magnitude as a comparable calculation of the rate of spread of Neolithic agriculture from the Levant across Anatolia to southeastern Europe (Harris 1996b).

In recent decades there has been much controversy among archaeologists about the relative significance in explaining culture change of processes of diffusion and of independent (autochthonous) development. The debate has tended to become polarized between proponents of these two modes of explanation, and it has been particularly lively in discussions of 'agricultural origins'. In this paper an attempt has been made to assess critically whether agropastoralism originated independently in western Central Asia or spread there from the Fertile Crescent. The evidence presently available decisively supports the hypothesis that it spread mainly by colonization during the 6th millennium bc across northern Iran within the belt of mediterranean climate that extends eastward past the Caspian Sea.

Acknowledgments

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The Spread of Agriculture to the Eastern Arc of the Fertile Crescent: Food for the Herders - F. Hole

Introduction

The link between the Böling-Alleröd amelioration, the Younger Dryas cold period, and the advent of agriculture and animal domestication seems well established (Hole 1989, 1996; McCorriston and Hole 1991; Moore 1992; Moore and Hillman 1992; Bar-Yosef and Meadow 1995). In this paper I discuss the spread of agriculture from its apparent heartland, the southern Levant, across the Fertile Crescent, into the Zagros. The timing of this expansion was determined by the climatic/environmental changes during the Climatic Optimum which immediately succeeded the Younger Dryas. At least for the eastern side of the Near East, the spread of agriculture was closely related to the expansion of animal husbandry and the development of patterns of seasonal transhumance.

We should bear in mind that "Late Quaternary paleoclimatic data available for Southwest Asia and the Near East are outstanding neither in quality nor in quantity" (Roberts and Wright 1993). Although much remains to be discovered about the precise nature of climate at any time or any place in the Near East during the crucial millennia, the broad outline and implications can now be sketched. Paleoclimatology has advanced more rapidly than archaeological discoveries which now lag seriously behind, both because of the inherently slow pace of excavation and analysis and also because many parts of our topical region have been inaccessible to modern research for prolonged periods. Further, the field of archaeology is notoriously underfunded so that skilled research teams can seldom sustain their efforts. An examination of the pattern of discovery reveals significant gaps in geographic coverage and an embarrassingly thin network of sites that span the crucial periods. However, notwithstanding such caveats, one can perceive an outline of the way agricultural economies spread across the

Near East.

More than 30 years ago, I was involved in the excavations that first recovered plant remains through the use of flotation, from an early village in Iran (Hole *et al.* 1969). Hans Helbaek, a pioneer in the technique of identifying plant remains and one of the first to apply his knowledge to the study of agricultural origins, examined this material from Ali Kosh (Helbaek 1969). He concluded that the site recorded some of the early attempts to bring cereals under human control. This unprecedentedly complete record, coupled with early radiocarbon dates, led us to believe that we had recovered some of the oldest evidence of domestication. We now know this to be untrue, although the local adoption of agriculture may have belatedly recapitulated similar events that took place earlier and repeatedly across the Fertile Crescent. Ali Kosh, on the Deh Luran Plain of southwestern Iran, lies near the southern edge of the Fertile Crescent, nearly as far from the southern Levant as one can get in the Near East. Despite the long geographic arc involved in travel, the Fertile Crescent probably provided the natural route for the spread of cereals and agriculture, although not by simple diffusion. Rather, the mountain zone also played an important role via transhumant pastoralism.

The spread of agriculture eastward

It is agreed that the first evidence of morphologically altered domesticated cereals is found at PPNA sites in the southern Levant: Jericho, Netiv Hagdud, Gilgal and Gesher, all clustered within a 15-km radius on alluvial fans in the Jordan Valley. The contemporary village of Aswad in the Damascus basin lies at the edge of what then was a marsh/lake. All these sites are dated to approximately 9000 BC calibrated (11,000 BP), just following the Younger Dryas cold interval which terminated ca. 9000 BC or a little later (Becker *et al.* 1991; Kromer and Becker 1993). Presumably there are other such sites in similar locations, most of them probably buried. Harlan notes that the Jordan Valley sites lie well below the oak woodland zone in which wild cereals occur today, as does Aswad (Harlan 1995), but he does not speculate about the distribution of trees 11,000 years ago when these sites were occupied. At Abu Hureyra on the Euphrates, Hillman reports finding both domestic and wild rye in late Epipaleolithic layers, as much as 500 years earlier than the occurrence of domestic grains in the southern Levant. Until the dating is confirmed, the next oldest site with plant remains in the Euphrates region is Jerf el-Ahmar, dated to 9000 BC. Here, wild barley, rye and einkorn were harvested but there is no evidence of the cultivated varieties (Wilcox 1995). The first actual domesticates on the Euphrates appear in Halula no earlier than 8000 BC, a full 1000 years after their occurrence in the Jordan Valley.

Much farther to the east, in the Tigris drainage of eastern Anatolia, the earliest settlement at Hallan Çemi dates to about 10,500 BC and lay in what may have been a refuge for pistachio and oak trees during the Younger Dryas (van Zeist and Bottema 1982; Rosenberg and Davis 1992; Rosenberg 1994). Despite this, no trace of cereals has turned up in the voluminous flotation samples. In other words, it appears that cereals were not part of the oak-pistachio-almond complex at this location and that this site - like contemporary Natufian sites - represents sedentism without agriculture. I have speculated that tree fruits provided much of the villagers' sustenance, in the absence of cereals (Hole 1996). By 9000 BC, after the Younger Dryas, Qermez Dere, located on the upper Mesopotamian Plain just south of the Jebel Sinjar, lay within the cereal belt, for the presence of einkorn, barley, legumes and pistachio nuts was reported (Watkins 1990). The first sites on the Jezireh Plain may have benefited from the massive increase in carrying capacity that the spread of wild cereals engendered (Hillman 1996). Whether cereals were present or not, each of these sites fits with the same late Epipaleolithic pattern of hunting and gathering in relatively rich environments which is manifest in the southern Levant among Late Natufian sites, and on the Euphrates at Abu Hureyra, Mureybit and Jerf el-Ahmar. The presence or absence of sites in any particular region before, during and after the Younger Dryas no doubt depended on the relative richness of local resources. Only after the Younger Dryas were rich resources widely spread.

In the Zagros the first known settlements were Zawi Chemi and Shanidar Cave, both of which are considered to be 'proto-Neolithic'. These sites, which were occupied during the onset of the Younger Dryas, were situated, like Hallan Çemi, in a forest refuge (Solecki 1981). In each case, occupation terminated during the Younger Dryas. It took another 2000 years before the first settlements appear in the true interior uplands. The first of these, Asiab, is a long-term but seasonal hunters' camp which carries on in the Epipaleolithic tradition (Braidwood *et al.* 1961; Bökönyi 1977). Significantly this is the last indication of such an adaptation. True agricultural villages also appear in the uplands of the Zagros at about the same time, as exemplified by Ganj Dareh at 8000 BC and Abdul Hosein, probably a little later. This first evidence of agriculture in the Zagros occurs 1000 years later than in the Levant. Both agriculture and stock-raising are attested at these Zagros sites which lie near the modern environmental limits for agriculture, and while neither enjoys a broad expanse of good alluvial soil, both have excellent access to still higher pastures. Ganj Dareh is a tiny site at 1400 m elevation, filled in part with small cubicles that impress one more as storage containers than as dwellings (Hole 1987a). Abdul Hosein at 1600 m asl is higher still, but it may actually be substantially later than Ganj Dareh (Hole 1987b). However, settlement of the eastern arc of the Fertile Crescent was anything but even. Jarmo and Ali Kosh, with locations that seem more favorable than those of Ganj Dareh or Abdul Hosein, were founded 1000 years after those sites.

A series of early villages with pottery, dating to around 6000 BC, is found in the intermediate valleys. One of these, Sarab in the Kermanshah Plain, gives evidence of initially having been a camp of transhumant herders who did not practise agriculture, at least in this location (Braidwood *et al.* 1961; Hole 1987a). The contemporary site of Guran in a nearby valley shows a similar practice of early herding followed by settled agriculture (Mortensen 1963, 1972). That transhumance was practised in the past is indicated by the occurrence of Neolithic sherds typical of Deh Luran, in mountain caves and shelters (Hole and Flannery 1967). The finding of a camp area used around 6000 BC by tent-dwellers would appear to solidify the case for systematic transhumance at that time (Hole 1974; Pires-Ferreira 1977), but we cannot say whether the practice dates back to the preceramic periods. This evidence, limited though it may be, suggests that the initial penetration of the Zagros was by herding people who carried agriculture with them seasonally to their summer pastures and then to their winter camps below the tree zone in the Fertile Crescent.

The climatic environment

There are no analogs for the climatic conditions that existed at the time agriculture began and spread. This is well illustrated empirically by the recent work on the Euphrates where, in the 11th-10th millennia (uncalibrated), the vegetation included rye and einkorn, along with arboreal species such as *Pistacia, Rhannus* and *Quercus,* which are adapted to cooler, wetter conditions than exist today. "The Neolithic vegetation resembles neither the surrounding steppe nor the Mediterranean vegetation to the west. It appears to correspond with more continental zones at higher altitudes" such as are found today above 800 m (Willcox 1996). Blumler (1996) also reminds us that "species which associated with each other in the past do not do so today and vice versa." Further, that "present-day plant communities almost certainly were not identical 10,000 years ago, and that whole communities did not shift north and south, or up and down slope, as climate changed. Rather, each individual species shifted location according to its own requirements and adaptations, forming new species groupings" (Blumler 1996).

Pollen profiles which reflect vegetational changes are the principal source of information about past climates in the Near East. These show that "essentially modem" conditions had been established throughout the Near East by around 6000 years ago (van Zeist and Bottema 1991; Roberts and Wright 1993). This date coincides with the termination of rapid sea level rise and with the attenuation of the Climatic Optimum. Since that time there have been relatively minor changes in global climate despite perturbations that sometimes had significant local effects.

Hillman has recently provided a detailed interpretation of the pattern of vegetational changes as they relate to agricultural potential. He refers to enormous increases in carrying capacity when cereals invaded the steppe and he traces this movement from its inception in the northwest Levant ca. 13,000 BC and its spread eastward to Zeribar at ca. 9000 BC (Hillman 1996). He argues that pistachio and almond trees were followed in succession by oaks. Cereals came in with the former, he says, and stayed with the latter. He sees oaks migrating at a rate of 150-200 km/millennium and terebinth at 200-300 km/millennium (Hillman 1996). He maintains that the forest is ecologically linked with the grasses which "spread together with (or slightly behind) the first terebinths" (Hillman 1996). Although this association is clearly manifest today, it may not have been so tightly linked in the past, as the evidence from Hallan Çemi suggests. In the Anatolian Tigris drainage, there was a relict forest with pistachio-almond but there is "a relative paucity of wild grasses" although pulses are common (Rosenberg 1994).

Another version of regional vegetational change is given by El-Moslimany (1983, 1986, 1994) who sees summer rainfall as a significant factor during the Climatic Optimum. In her scenario this resulted from a shift in the ITCZ northward to near the head of the Gulf (El-Moslimany 1983). As evidence she cites Gramineae in peat deposits from Bubiyan Island at the head of the Persian Gulf, as well as Poaceae/Chenopod+*Artemisia* ratios in the Zagros pollen cores. The early Holocene records uniformly indicate much higher percentages of grass (Poaceae) than are found in surface samples today, even in areas protected from grazing (El-Moslimany 1994). Since "grasses play a dominant role in vegetation only where there is adequate moisture during the growing season" and "grasses adapted to summer aridity produce less pollen than those growing in regions of summer precipitation" she infers that a high P/C+A ratio implies warm-season precipitation. Using this line of reasoning she finds that summer precipitation extended to northern Mesopotamia; for example to Mureybit on the Euphrates where "Poaceae pollen reaches 60-70% of the total pollen between 8000 and 7600 BP" whereas today it "comprises only 3.8% of modern samples" (El-Moslimany 1994). El-Moslimany concludes that "even at its maximum, summer rainfall was probably only a small percentage of total annual precipitation" (El-Moslimany 1994). She sees a shift throughout the region to dominant winter rainfall after 6000 BP.

El-Moslimany, as well as Roberts and Wright (1993), highlight the differences during the Climatic Optimum - especially greater seasonal contrast in temperature and increased precipitation, both of which impacted primary production and reinforce the conclusion that there are no modern environments strictly comparable with those when agriculture spread.

The spread of agriculture

Agricultural origins were restricted to a narrow strip of land along the eastern Mediterranean because that is one of the few places (the only place?) where annual cereals grew until the Climatic Optimum. Once agriculture had begun, it could spread through diffusion to indigenous people (Harris 1996), or perhaps have been 'invented' repeatedly, or introduced by emigrant colonizers. The mode of transmission in different parts of the Near East may have differed and each region requires its own explanation. My focus in this paper is on the Zagros, the easternmost region of the Near East.

First we must recognize that there is a vast territorial gap stretching across northern Mesopotamia, from the Euphrates to the Tigris, in which no early agricultural communities have yet been found. Although this represents one of the most fertile and agriculturally productive parts of the Fertile Crescent today, it seems not to have played a role in the early development or spread of agriculture. Between the sites on the Euphrates and the pre-agricultural settlements of Hallan Çemi, Qermez Dere, Nemrik 9 and M'lefaat in the Tigris drainage, there is no evidence for extensive human use of this steppe before the PPNB in the 9th millennium BC.

The evidence from the Deh Luran Plain in southwestern Iran is consistent with the general picture of agriculture spreading along the pistachio-almond fringe of steppe, for the earliest community was apparently situated on such a steppe, but immediately alongside a marsh (Helbaek 1969; Kirkby 1977; Woosley and Hole 1978). Nevertheless, one is struck by the fact that this settlement is 1000 years younger than Ganj Dareh. The principal cultivated crops at Ali Kosh were emmer wheat and einkorn, but there was also a minor component of two-row hulled barley. By quantity, however, most of the plant remains consisted of wild legumes and grasses, perhaps collected not for human consumption but for fodder (Miller 1984, 1996). This inference is supported by the presence of domestic goats and sheep which arrived in Deh Luran with the earliest agriculturalists. There is little doubt that the entire agricultural complex reached Deh Luran as a package, albeit one not committed only to the domestic species of either plants or animals. Agriculture assumed greater importance in the ensuing centuries as the marsh began to dry up. By the time the site was abandoned a little after 6000 BC, *Prosopis* had come to dominate the landscape and evidence of agriculture is sparse compared with herding. This is intriguing because *Prosopis* may not have been an indigenous plant. Rather, its home may have been in the mountains from which it was transported in the feces of domestic herds (Helbaek 1969).

We pick up the thread of continuity at Chagha Sefid (ca. 5800 BC) whose pollen shows a mix of wet and dry plants of the types found in ditches rather than in marshes. Flax also appears in significant amounts, suggesting either greater precipitation than today or the importation of the plants. The faunal remains give a strong impression of specialized herding. True irrigation arrives in the succeeding phase, after which plants typical of supplementally watered fields occur. The settlements of Chagha Sefid and Tepe Sabz came to an end in the mid-5th millennium BC when there was a reversion to steppe-like conditions similar to those obtaining at the termination of Ali Kosh (Hole 1977).

If agriculture actually was earlier in the mountainous zone, as evidence suggests, it supports the suggestion that crops such as emmer as well as wild vegetation such as *Prosopis,* mallow and perhaps flax were introduced to Deh Luran from the uplands as Helbaek inferred. There is good ecological reason to support this scenario: namely, seasonal transhumance between mountains and plains to provide equable climate and forage for herded animals. Thus, in the Zagros we may see the spread of agriculture as part of a process of extending herding territories. In other words, the impetus for the spread of agriculture was to provide food for mobile herders.

Herding and agriculture

The hypothesis that agriculture was spread across the Jezireh and down the Zagros by herders depends on a combination of empirical evidence, climatic interpretations and ethnographic analogy. The empirical evidence and climate are summarized in Hole (1996) and the ethnographic sources include Digard (1975, 1981), Hole (1977, 1978, 1980) and Watson (1979).

In essence, the argument is that herding arose in the foothills of the Zagros/Taurus at a site like Hallan Çemi which was nestled in a forest refuge during the Younger Dryas. The voluminous and high-quality botanical remains show intensive use of tree fruits such as almond and pistachio, but there are no apparent cereals in the environment. Both humans and potential sheep/goat domesticates would have congregated around this 'oasis'. Because of the severity of the weather during the Younger Dryas, forage for these ungulates may have been restricted to the lower elevations. As the caprines are genetically disposed to follow leaders, it was relatively easy to bring captured infant animals under control (Geist 1971). When the climate ameliorated, potential pastures opened and the caprines could be herded to take advantage of them. The new climatic regime, with its summer temperatures higher than today's, created inviting environments in the uplands while rendering the lowlands less desirable. During the winter, the reverse situation obtained and the lowlands afforded warmth and shelter. In other words, climate and the seasonal growth of vegetation favored vertical transhumance whether people were herding and farming, or hunting and collecting wild foods.

The admittedly sparse evidence presently supports the hypothesis that the uplands were first colonized by hunters and herders as at Asiab and Ganj Dareh. The herders carried with them the newly arrived cereals from the lowland steppe, which they planted in upland fields as supplements to the autumn harvest of tree fruits. Because the climate in the 10th to 9th millennia was considerably warmer and wetter in the summer, herders were able to establish crops in valleys that today are near the limit for agriculture, such as Ganj Dareh. Because of the severe winters then, transhumance would have been favored over permanent settlement. Winter sites in the lowlands or sheltered lower valleys must also have been favored. This is precisely the pattern followed by herding people in recent times, many of whom also planted small fields in each of their seasonal territories.

According to this hypothesis, the initial entree into the Zagros exploited the grazing potential of the upland regions in the summer and retreated back into the oak/pistachio/almond zones during the winter where gathered tree fruits could sustain the carbohydrate needs of the people. In time, this tree zone moved farther and farther south along the front of the Zagros, thus providing new opportunities for winter camps of herders. According to pollen evidence, trees were only fully established at Zeribar around 6000 BC. Topography also played a role in where people settled, for routes permitting vertical transhumance (east-west movement) are scarce along the Zagros front, and travel in the mountains is easiest in alignment with the mountain ridges (NW-SE). These routes along linear valleys are also excellent pasture, lacking principally dependable sources of surface water (Hole 1962; Hole and Flannery 1967). For these reasons, a model of simple diffusion, plotting time against distance, is not realistic, for the Fertile Crescent is not an isotropic plain, and the Zagros/steppe zone does not have a uniform distribution of resources. Only by factoring in these environmental differences and the ways people exploited them can we perceive an accurate picture of the way agricultural economies became established in this remote zone some 2000 km from the source.

We should also consider the intervening region, the Jezireh Plains between the Euphrates and Tigris Rivers. There are no early villages known except on the easternmost flank of this region (i.e. Qermez Dere, M'lefaat). One may speculate and offer some hypotheses that are testable. Hillman sees an extensive forested zone, albeit park-like, a zone that would appear on the surface to afford unusually rich opportunities for early agriculturalists, as well as to provide an abundance of wild foods. One might argue that the very richness of the environment precluded agriculture, but would encourage sedentary living; however, in the absence of villages like Qermez Dere or Hallan Çemi, such an argument lacks force. Although the presence of 7th millennium sites such as Umm Dabaghiyah, well outside today's agricultural zone in Iraq, implies a much broader region in which cereals could grow during the Climatic Optimum, despite extensive surveys in Syria, similar sites have not been discovered. An alternative view would be that despite the veritable sea of cereals stretching from horizon to horizon, life on the open steppe was unattractive because of predators and the risk of uncontrollable fires when the vegetation was dry. The lack of permanent streams and rivers (no doubt a factor of greater significance today than it was following the Younger Dryas) would also have determined the spacing and density of settlements. Finally we may consider whether, because of higher summer temperatures, the prevailing pattern of adaptation was one of only seasonal use. Perhaps more substantial remains are to be found in the Taurus foothills.

Conclusions

This paper has highlighted some of the essential differences between the Levant and the northern Jezireh and the Zagros arc. Geographically the lands between the coastal range and the Euphrates share a lowland contiguity and adaptation which is reinforced by numerous shared cultural attributes. To the east of the Euphrates the Fertile Crescent merges with the Taurus and Zagros mountain ranges which offer a wide range of plant and lithic resources and, through vertical transhumance, a means to extend the growing and harvest seasons over several months and even to enjoy two distinct harvest seasons in spring and fall. The differences between plains and mountains encourage seasonal rather than year-round occupation, and extensive rather than intensive utilization. These factors combine to discourage the growth of agricultural villages and favor instead transhumance centered around the needs of livestock. The initial spread of agriculture in this northern and eastern arc of the Fertile Crescent was intimately tied to these seasonal movements.

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Early History of Sesame Cultivation in the Near East and Beyond - D. Bedigian

Introduction

Sesame (*Sesamum indicum* L.) was cultivated in ancient India, Sumeria, Egypt, Anatolia and throughout the Greco-Roman world both for its edible seed and its oil (Bedigian 1985; Bedigian and Harlan 1986). It is often described as the oldest oilseed plant used by humans (Joshi 1961; Weiss 1971). However, there has been some confusion about its origin which has been discussed by Nayar and Mehra (1970), Nayar (1976) and Bedigian (1984).

A group of wild and weedy forms native to India and described as *Sesamum orientale* L. var. *malabaricum* Nar. shows close morphological, genetical and phytochemical affinities to the cultivated crop. Bedigian (1988) and colleagues (Bedigian *et al.* 1985, 1986) have provided evidence to support the theory that domesticated sesame arose from this progenitor on the Indian subcontinent. Zohary and Hopf (1993) concurred with Bedigian and Harlan (1986) that the botanical evidence supports a relatively late introduction of sesame into the Near East and the Mediterranean region. The genus is restricted to the Indian subcontinent, where there are only a few wild species, and to Africa south of the Sahara, where there are numerous wild species.

The archaeological record

1. The Indian subcontinent: Harappa

The oldest remains of sesame seeds were found at the Indus Valley civilization site of Harappa (Vats 1940) in Pakistan, where excavators uncovered "a quantity of lumped and burnt *Sesamum* specimens." Vats (1940) dated the sesame to about 3050-3500 BC. Weber (1991) does not list sesame among the finds at Rojdi, but his review indicates that sesame was first found in the 'Indus Valley Core Area, Mature H' phase that he attributes to ca. 2600 BC, and that sesame was planted as a summer crop. This is probably the area where the plant was first cultivated.

2. The pre-classical Near East

Mesopotamia

To date, no sesame seeds have ever been recovered from excavations in Mesopotamia.

Egypt

The rediscovery of sesame seed remains from King Tutankhamen's tomb (ca. 1350 BC), which was discovered in 1927 by Howard Carter, pushes back the date of the earliest record of sesame seeds in the Near East (de Vartavan 1990). Some 30 boxes of plant remains associated with the burial of King Tutankhamen were stored at the Royal Botanic Gardens, Kew, England, where botanist Leonard Boodle worked on cataloging these specimens until his death in the 1930s.

Recently C.L.T. de Vartavan, a graduate student, went through these boxes and examined their contents. He found about 60 ml of sesame seeds which were the main ingredients of one of the many containers in the tomb's Annex filled with food, drinks, ointments, perfumes and oils. The sesame was originally stored in one of the 116 reed baskets containing seeds and fruits. The basket was oval-shaped. These seeds represent the only find of sesame seeds ever recorded from investigations of ancient Egypt, as well as the earliest sesame from the Near East and Africa.

Armenia

Remains of sesame seeds dating between 900 and 600 BC have been found at Katmir Blur, an early Iron Age Urartian site on the outskirts of Yerevan. Four large jars containing carbonized sesame seed were excavated. Elaborate devices for oil extraction indicate that the Urartians processed the sesame seeds for oil (Piotrovskii 1950, 1952; Kassabian 1957; Bedigian 1985; Bedigian and Harlan 1986). Another find from the same era comes from the Kingdom of Urartu, Bastam, in Van province of eastern Turkey (Hopf and Willerding 1989).

Jordan

About 200 sesame seeds dating from ca. 800 BC were uncovered at Deir Alla site in the Iron Age beds (Neef 1989).

Turkey

Sesame seeds were recovered at the Gordian ruins in Anatolia during the 1989 excavation of the 'Destruction Level' (ca. 700 BC). The seeds are from a pure sample (about 250 ml) from within a pot that was sitting on the floor (along with other pots containing wheat, barley and lentil). Massive burning and the collapse of the roof seem to have effectively sealed the contents on the floor (N. Miller, pers. comm.).

Early historical records

1. The Indian subcontinent

The fact that the Sanskrit words for oil and sesame are the same suggests that sesame may be one of the earliest oil-bearing plants to be brought under cultivation (Sampson 1936). The words ('tíla', 'jartíla', 'tilpínja', 'tilapíñjí') all occur in old Vedic texts dating from ca. 1000 to 800 BC (F.J.B. Kuiper, pers. comm.)

Tíla has been employed in religious ceremonies from very early times. It was regarded as holy (Hopkins 1968), and an offering of tíla seeds was considered effective in removing sins (Gupta 1971). Offerings of water and sesame were said to free an individual of all debts of his ancestors.

2. The Near East

Mesopotamia

Early Old Babylonian (OB) documents contain numerous references to "i-gis = ullu/ellu, the ubiquitous sesame oil" (Simmons 1978). Texts list the expenditure of sesame oil "for inner bolt", "for the fire offering", "for the Price", "for the royal purification rite", "for the inner bolt on the day of Akitu", "for the sizkur divine name", "for the Elunum divine name", "for the regular offering" and "for anointing the banner." These are all special cultic applications which employed sesame oil to lubricate, soap or fuel someone or something, almost certainly at springtime festivals (W. Doyle, pers. comm.).

The *Assyrian Dictionary of the Oriental Institute,* Chicago, better known as the *Chicago Assyrian Dictionary* (*CAD*)*,* edited by Oppenheim *et al.* (1958), provides a definition for ellu as: "[C]lean, pure in connection with oil, etc.,...fine oil...sweet oil...pure sesame oil, sesame oil of the first [pressing]," used for anointing and making perfume. Another definition is: '[H]oly, sacred'.

The samassammu article prepared for the CAD's 'S' volume (Reiner 1989) mentions several texts that help to identify samassammu as sesame. An OB text concerned with processing the seed says: "it came to 90 gur of samassammu, before it started raining. I managed to crush 40 gur of it and the rain did not arrive to ruin it" (Dossin 1933). The average distribution of the rains in Mesopotamia falls in autumn, thus the text refers to a summer crop that was harvested in the fall.

The article itself contains many references to oil-processing, including one text cited in CAD that specifies samassammu pesutu (as white samassammu). The texts concerning white-seeded samassammu provide evidence of considerable importance in helping to distinguish flax from sesame because there are no flax cultivars with white seeds. This article contains other references to se-gis-i as food for the royal meal, as a medicine, and as an ingredient (along with alkali and juniper resin) in soap-making.

Stol (1985) indicates a textual reference to 'sweet' matqutum (sesame) that reminds us of the folk classification by Sudanese farmers. Sesame used for its seeds was called 'sweet', while sesame grown for its oil was considered to be 'bitter' (Bedigian and Harlan 1983). Often, the red-seeded sesame cultivars had the highest oil content, but the testae probably contained high levels of tannins or other bitter-tasting constituents. The 'sweet' sesame was white-seeded.

A fragment of a Neo-Assyrian textbook tablet concerns the problem of ants in a storage bin with samassammu: "if ants are seen in a man's house" "in the storage bin for samassammu" (Ebeling 1923 cited in CAD). This may be coincidental but might have considerable significance, in view of the role of lignans of sesame as insecticides (Bedigian *et al.* 1985).

An argument put forth at the Sumerian Agriculture Group's 1984 meeting at Trinity College, Cambridge against identifying sesame as the ancient oilseed was based on a text that described the harvesting of samassammu by uprooting the plant. Some participants argued that flax alone was harvested in this way. However, during May 1997, the previous season's dried sesame stalks saved for kindling in villages along the Euphrates from 100 km north to 100 km south of Deir Zor were examined. In more than half of the fields in the villages visited, sesame had been harvested by uprooting the entire plant.

Egypt

The earliest textual reference to sesame dates from 256 BC (Lucas 1962). Both sesame and sesame oil are mentioned in the Tebtunis Papyri 3 (part 2, No. 844). Select Papyri (Hunt and Edgar 1932) mention sesame paste oil, and seeds. Deines and Grapow (1959) indicate that sesame was used as a medicine. Pliny (1938) wrote that a large amount of oil in Egypt was obtained from gingelly (sesamum).

The difficulty is to identify the ancient words for sesame. There is a striking linguistic resemblance of the Mesopotamian word samassammu to related Near Eastern terms, such as the Arabic word 'simsim' and the name of a plant with edible seeds that is transcribed 'smsmt' (Germer 1979). Loret (1892) regarded the Coptic name for sesame, 'oke', as Egyptian in origin. Another word from the hieroglyphs, 'ake', referred to a plant that produced oil and whose seeds were used medicinally. 'Ake', then, could be the Egyptian name for sesame (Loret 1982). But whether this later became oil of the highest quality, which was 'nhh', which one encounters from the 19th dynasty (1320-1200 BC) onward, remains a mystery. The assertion of some authors that 'nhh' was *Ricinus* oil has been disputed on the grounds that castor oil is unpalatable (Keimer 1924) and also toxic.

3. Classical Greece

Historical sources

Sesame was cultivated extensively in the Greco-Roman world, but more for its edible seed than for its oil. The writings of Greek travelers and historians provide some clues to the cultivation of sesame in the ancient world. These records make it clear that sesame was well known in Mesopotamia by the time of the Iron Age. Herodotus, in the 5th century BC, observed that the only oil the Babylonians used was from sesame (Herodotus 1928).

The cultivation of sesame in ancient Armenia was documented by Xenophon (1901) in the 5th century BC. In the book *Anabasis,* he wrote: "In (western Armenia)... there was a scented unguent in abundance that they used instead of olive oil, made from pork fat, sesame seed, bitter almond and turpentine. There was a sweet oil also to be found, made of same ingredients." Xenophon also placed sesame in two other parts of Anatolia. One was Cilicia - "[t]his plain produces sesame plentifully, also panic and millet and barley and wheat" - and the other was "Calpe Haven in Asiatic Thrace" farther west. "Calpe lies exactly midway between Byzantium and Heracleia" has "good loamy soil... produces barley and wheat, pulses of all sorts, millet and sesame, figs in ample supply, numerous vines... indeed everything else except olives."

Botanical sources

Theophrastus (1916) identified sesame as one of the main summer crops of his time along with millet and Italian millet, erysimon and horminon, in the 4th century BC (Bedigian and Harlan 1985; Gallant 1985).

4. Imperial Rome

Cultivation requirements

Columella (1941) reported accurately that in the 1st century AD "it [sesame] usually requires loamy soil, but it thrives no less well in rich sand or in mixed ground... But I have seen this same seed sown in the months of June and July in districts of Cilicia and Syria, and harvested during autumn, when it was fully ripe." He also wrote that "[i]n some districts (of Anatolia) such as Cilicia and Pamphylia, sesame is sown this month (late July to August); but in the damp regions of Italy it can be done in the last part of the month of June." This report might indicate that like the Babylonians, the Cilicians and Pamphylians grew sesame as a second crop after harvesting barley or another earlier crop.

Trade

Travel and trade on the Indian Ocean were described by an anonymous merchant of the 1st century AD in *The Periplus of the Erythraean Sea* as follows: "Ships customarily fitted out from places across this sea, from Ariaca and Barygaza, bringing to these far-side market towns the products of their own places; wheat, rice, clarified butter (ghee), sesame oil, cotton cloth and girdles, and honey from a reed called saccharum. Sesame oil was traded along with cloth and wheat, for frankincense." However, India occupied a unique position in the commercial world as an important supplier of luxury goods long before this document was written (Mookerji 1912; Ratnagar 1981).

Pliny (1938) also wrote in the 1st century AD that "[S]esame comes from India", and that it is a summer grain to be sown before the rising of the Pleiades. "We have specified gingelly (sesamum) and common and Italian millets

as summer grains. Gingelly comes from India, where it is also used for making oil; the color of the grain is white." Pliny appears to be accurate and he seems to have known sesame well. His advice for soaking sesame seeds prior to milling is reminiscent of practice in Urartu: "Gingelly is to be steeped in warm water and spread out on a stone, and then rolled well and the stone then dipped in cold water so that the chaff may float to the top, and the chaff again spread out in the sun on a linen sheet, before being rolled again." In addition, Sturtevant (1972) stated that the Romans ground sesame seeds with cumin to make a pasty spread for bread.

5. Urartu

Based upon his participation in the excavation of an oil-extraction workshop at the Uratian site of Karmir Blur near Yerevan, Kassabian (1957) reconstructed Urartian techniques for sesame oil production as follows: sesame reserves were brought to the oil press. They were washed in a basin-shaped stone container, 79 cm in diameter, carved from a block of tufa. The basin joined a cylindrical pipe made of the same stone, which allowed waste liquid to drain out beyond the citadel. Sesame seeds were soaked to ease the removal of the tegument. After maceration and thorough pressing, the sesame was moved in a semi-moist condition to the oil press (workroom #2). Here they pounded the sesame using mortars and pestles.

Details about the plant remains and tools uncovered at Karmir Blur are summarized by Bedigian and Harlan (1986). The workrooms were furnished with fireplaces for parching the seed. Other finds included clay storage jars 1.5 m tall, cakes of pressed sesame (the solid residue that remains after seeds are crushed for oil), and stone mortars, pestles and graters.

6. Armenia

The word for sesame in the Armenian dictionary is 'shushmah' (Yeran, undated), not unlike the Sumerian word samassammu (Charles Perry, pers. comm.). The second Armenian word for sesame is 'kunjut'. Friedrich Parrot travelled in Armenia more than 150 years ago, and described the cultivation on the Araks River Plain. In the Araks basin, near Yerevan, the capital of Armenia, grew field crops including cotton, castor, melons, pumpkins, tobacco, wheat and barley. Parrot noted that "the plant, however, which is of greatest importance to Armenians, on account of their fasts, is the 'kunjut', from the diminutive seeds of which a well-flavored oil is prepared, and used as a substitute for butter" (Parrot 1845).

7. Arabia

Language

Gingelly, a name for sesame that is often used today in India and Europe, is derived from the Arabic word 'juljulân' (Dymock *et al.* 1893; Gove 1967). Spaniards say 'ajonjoli', the French 'jugleone' and the present-day Arabic medicinal and botanical works employ both 'al-juljulân' and 'simsim'. The word 'juljulân' was in use by the 8th century, as evidenced in a poem (Faroukh 1965); 'juljulân' had the meaning of tiny seeds, and sesame was a plant proverbial for its production of tiny seeds (Charles Perry, pers. comm.). But 'juljulân' is usually defined as the sesame capsule before the seeds are removed. Abu Al-Gauth said "Al-juljulân is sesame in its hull [or peel], before it is harvested." However, Charles Perry, a specialist in Near Eastern languages, has discussed the relationships among the various terms. He observed: the Hebrew word 'shumshom' (mentioned in the Mishna but not in the Bible), Aramaic 'shushma', Armenian 'shusham', Turkish 'susam', Arabic 'simsim', Greek 'sesamon' and the rest go back to the word recorded in Sumerian. However, whether it is really of Sumerian origin or borrowed from Akkadian, the Semitic language spoken by the Sumerians' neighbors, is a moot question. There may have been borrowings in both directions. But in the Arabian Nights when Ali Baba says "open sesame" he actually says "iftah, ya simsim."

Symbolism in legend

The Sudan Department of Agriculture and Forests and the Department of Economics and Trade bulletin on sesame (1938) opens with a concise version of the story of Ali Baba and the Forty Thieves: "When the robbers had departed Ali went to the door of the cave and pronounced the magic words he had heard them use, 'Open Sesame'. The door opened and he went inside and the door closed behind him. So astonished was he at the sight of the treasures in the cave and so absorbed in contemplation of them that when at last he desired to leave the cave he had quite forgotten the magic word 'Sesame'. In vain he cried out loud 'open wheat, open barley, open maize, open lentils'; none of these availed and the door remained shut."

The significance of sesame in Arab culture is suggested by the fact that it was chosen as a magical means of commanding access (Arulrajan 1964). Once, sesame was thought to have mystical powers, and it still retains a magical quality. In fact, 'Open Sesame' has become a common cliché that is still in use today. But why sesame? The answer may lie in the high quality of sesame oil which could have thought to act magically on door locks so

that they open easily; in addition, sesame capsules do dehisce spontaneously (magically?) to release their seeds.

8. Persia

Symbolism in legend

Another example of the use of the word sesame comes from Persia. It occurs in the book *Iskandarnama* (or the *Book of Alexander*), one of the *Sharafnama* or the *Book of Kings,* which was completed in 1010 AD. Accompanied by a miniature painting of Alexander feeding sesame seeds to birds, the story relates the parleying before battle between Alexander and Darius III of Persia around 330 BC. It seems Darius was offended since Alexander had not sent him gifts in the traditional manner and despatched a messenger to tell him so. Alexander, equally angry, replied that Darius had treasure enough already. Whereupon Darius, furious by now, sent Alexander a polo stick with a ball and a bowl of sesame seed saying that since Alexander behaved like a child he should have the playthings of a child. The sesame seed, however, represented the countless soldiers in the great Persian army which Darius proposed to send against him. Alexander chose to interpret the gifts in somewhat another way and saw them as omens of victory. To him the polo ball represented the world (i.e. Darius' possessions) which Alexander would draw toward himself with the stick (i.e. by means of his army) as in the game of polo. He threw the sesame seeds to the birds which pecked every one of them from the ground and told Darius' messenger that it would be thus that his soldiers would wipe out the army of Darius. He then sent the messenger back to Darius with a bowl of mustard seed as a symbol of his own soldiers. The miniature graphically portrays this incident with a flock of hoppoes, parrots, pigeons, starlings and crows pecking the seed watched by Alexander and his retinue while the polo sticks and bowl of remaining seed are in the background (Titley 1979).

Conclusions

There is botanical and textual evidence for cultivation of sesame (described in the literature as *Sesamum indicum* and *S. orientale*) in the ancient Old World. Excavations at the Indus civilization site of Harappa have yielded charred sesame seed from a stratum attributed to 3050-3500 BC. The Vedic scriptures contain frequent references to sesame. The existence and identity of S. *indicum* as a Mesopotamian oil source have been controversial since 1966 when H. Helbaek reported that not a single seed of sesame had been found in the Near East from earlier than Islamic times. The Chicago Assyrian Dictionary and some cuneiformists subsequently have translated 'se-gis-i' (Sumerian) and 'samassammu' (Old Akkadian) as 'linseed' (flax). Helbaek's assertion that no ancient sesame remains have been excavated is inaccurate, but the reported finds (King Tutankhamen's tomb; Karmir Blur in Armenia, the ancient Urartu; Gordian in Turkey; Hajar bin Humeid in South Arabia) are late. Sesame was a major item of agriculture in the Urartian economy and that kingdom was a northern neighbor of Mesopotamia.

Herodotus wrote that sesame was the only oil used in Babylonia. The crop was well known to ancient Greek and Roman authors. The most helpful ancient sources are cuneiform texts which indicate that the barley harvest (in spring) was followed by the sowing of 'se-gis-i', a summer crop in Mesopotamia. Sesame can be distinguished clearly from flax, a cool-season crop, and their growing seasons differ as would be expected. New evidence collected in Syria, following the discussions at the May 1997 Harlan Symposium, supports my previous suggestion that the Mesopotamian oil plant is sesame. A survey of villagers 100 km north and south of Deir Zor in Syria told me that they would be planting sesame once they finished harvesting barley in about a month and in more than half of the fields, sesame was harvested by uprooting the entire plant.

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Grain Legumes: Evidence of these Important Ancient Food Resources from Early Pre-agrarian and Agrarian Sites in Southwest Asia - A. Butler

Introduction

The beginnings of plant food production in Southwest Asia are well documented, and a number of recent reviews have described the archaeobotany and the development of agriculture (for example Kislev 1992; Ladizinsky 1989; Miller 1991, 1992; Zohary 1989, 1992). The progression of plant exploitation from gathering to domestication has been examined and reassessed as new data have been published over the past ten years (e.g. Colledge 1994a, 1994b; Zohary and Hopf 1994; Garrard *et al.* 1996; de Moulins 1997). The archaeobotanical remains of pulses in particular have been reviewed by a number of workers including Hopf (1986), Zohary and Hopf (1973) and Kislev and Bar-Yosef (1988). The association of cereals with grain legumes has been well noted, and probably unsurprisingly these two important plant groups have commonly been considered in tandem as human food resources, often with the tacit assumption that they require similar

environmental conditions, and are exploited in the same manner. It has been suggested, largely from the properties of seed dormancy and pod dehiscence in the wild legumes, that the pattern of domestication of the pulses differed from that of the cereals (Ladizinsky 1987). Further, from the ecology, distribution pattern and nutritional properties, which favored them as a human food resource, the suggestion has been advanced that legumes were cultivated before cereals (Kislev and Bar-Yosef 1988). However, these views have been vigorously countered. The current opinion appears to favor parallel and probably synchronous developments toward domestication (Zohary 1989; Blumler 1991).

In the light of a recent reconstruction of the vegetational history and new archaeobotanical data with further radiocarbon dates, this paper looks again at the evidence of the pulses as human food resources prior to and at the beginning of domestication. The first part sets the background scenario where the effects of the major climatic changes following the last glaciation are outlined. This is followed by a brief update on the occurrence and distribution of the remains of grain legumes recovered from archaeological sites in Southwest Asia from the Epipalaeolithic to the early Neolithic and the beginnings of agriculture. The second part considers the environmental requirements of the legumes, and their habits. The properties that might have enabled this plant group to survive and succeed throughout the climatic fluctuations are sought, toward a greater understanding of the success of the pulses as early crop plants.

In this paper "bc" refers to uncalibrated radiocarbon dates, "BC" to calibrated dates. For the purposes of consistency, the dates are given throughout in the form of uncalibrated years before Christ (bc). The period discussed is between 17,000 and 5500 bc.

Environmental changes from the Epipalaeolithic to the Neolithic

The global climatic data which have been extracted from glacial and marine cores show that the glacial maximum occurred between 18,000 and 16,000 bc, followed by a gradual rise in sea level. At about 11,000 bc a more rapid rise in sea level indicated the start of a warmer, wetter period, the Bölling-Alleröd interstadial. However, by 9000 bc the climatic situation reverted to the cold, dry conditions of the Younger Dryas. This is estimated to have continued for 500 to 1000 years. This period was followed by a gradual climatic amelioration toward the Holocene and the conditions of the present day. Sea levels appear to have reached maximum levels by around 4000 bc (references cited in Sanlaville 1996).

Evidence that these changes affected the Levantine region has been derived from cores extracted from the Eastern Mediterranean basin (Nesterhoff *et al.* 1983; Thunell 1979; references cited in Sanlanville 1996). Sedimentary studies in the Levant have given further information. Analyses of cores taken from the bed of Lake Lisan, which once occupied part of the Rift Valley, and cores from the Negev and the Jordan Valley have shown that the climate between 12,500 and 10,500 bc was uniformly wetter than today. Between 9000 and 8000 bc the cold dry climate associated with the Younger Dryas is indicated in the Jordan Valley, with, however, some evidence that wetter conditions persisted further south in the Negev. This was followed by a general return to warmer, wetter conditions by 6500 bc (references cited in Goldberg 1994).

The pollen data from the Ghab Valley in Syria and Lake Hula near the Sea of Galilee, together with further pollen analyses from Lake Van in Anatolia, Lake Urmia in northwest Iran and Lakes Mirabad and Zeribar in the Zagros, have added botanical evidence to the climatic information (Baruch 1994).

Recently Hillman (1996) has constructed a detailed model for the vegetational history of the Fertile Crescent up to the Holocene, largely based on a synthesis of the above analyses together with pollen data from archaeological sites in the Levant (Leroi-Gourhan and Darmon 1991). Hillman's model follows the proposals of van Zeist and Bottema (1991) that during the last glacial period, the forest vegetation survived near the Levantine coast, and also in isolated patches scattered on higher ground not only in the northern Levant but also further east toward the northern Zagros. The steppe vegetation would have been characterized by the wormwoods, chenopods, leguminous shrubs, thistles and knapweeds, and possibly accompanied by perennial grasses. As warmer conditions returned around 13,000 bc the forest expanded from these refugia across the steppe and desert-steppe in the southern and northern Levant and also across the north of the Fertile Crescent, starting with the terebinths and wild fruit trees of the Rosaceae family, and then including the oaks. The archaeobotanical remains from Abu Hureyra in Syria show that some xeric woodland must have survived there until about 9000 bc. A retreat of the forest cover occurred again during the Younger Dryas, until perhaps 8200 bc toward the start of the Holocene, when again there was vegetation expansion and re-establishment. It is suggested that during periods of harsh climate, wild grasses and legumes would have survived in the coastal belt and woodland refugia, facilitating their subsequent expansion with the forest.

Table 1. Pulses and cereals recovered from Southwest Asian sites 17,000-5500 bc.

Site	Site and date	Area	Date	Wild	Domest.	*Lens*	*Vicia*	*Pisum*	*Cicer*	*L.*	*V.*	*Vicia*	Pulse

no.†			(bc)‡	cereals	cereals	spp.	*ervilia*	spp.	spp.	*sativus* type	*faba* type	spp.	
Fig. 1	**Epipalaeolithic (17,000-8500 bc)**												
1	Ohalo II	Levant	17,000	X	-	X	-	-	-	-	-	-	-
2	Wadi-el Hammah 27	Levant	10,200-9900	X	-	X	-	-	-	-	-	-	X
3	Hayonim	Levant	10,400-10,000	X	-	-	-	-	-	-	-	-	X
4	Abu Hureyra	Syria	9100-8300	X	X	X	X	-	-	-	-	-	X
Fig. 2	**PPNA (8500-7500 bc)**												
1	Jericho PPNA	Levant	8000-7300	-	X	X	-	-	-	-	-	-	-
2	Netiv Hagdud	Levant	7900-7600	X	-	X	X	-	-	X	-	-	X
3	Iraq el-Dubb	Levant	9100-7300	X	X	X	-	-	-	-	X	-	X
4	Gilgal	Levant	7900-7700	X	-	-	-	-	-	-	-	-	-
5	Tell Aswad I	Syria	7700-7300	X	X	X	X	X	-	-	-	-	X
6	Mureybit I	Syria	8500-8200	X	-	X	-	X	-	-	-	-	-
6	Mureybit II	Syria	8200-8000	X	-	X	-	X	-	-	-	-	-
6	Mureybit III	Syria	8000-7600	X	-	X	X	X	-	-	-	-	X
7	Jerf el Ahmar	Syria	7800-7700	X	-	X	X	X	-	-	-	X	-
8	Hallam Çemi	Turkey	8500-7500	-	-	X	X	-	-	-	-	-	X
9	Qermez Dere	Iraq	8000-7900	-	-	X	X	-	-	-	-	-	X
10	M'lefaat	Iraq	7800-7600	X	-	X	X	-	-	-	-	-	X
Fig. 3	**PPNB (7500-6500 bc)**												
1	Beidha	Levant	7100-6500	X	X	X	X	-	-	-	-	-	X
2	Nahal Hemar	Levant	6900-6300	-	X	X	-	-	-	-	-	-	-
3	Jericho PPNB	Levant	7300-6500	-	X	X	-	-	-	-	-	-	-
4	Yiftah-el	Levant	6900-6600	-	-	X	-	-	-	-	-	-	-
5	Ain Ghazal	Levant	7200-6500	-	X	X	-	X	X	-	X	-	-
6	Wadi el-Jilat 7	Levant	6800-6300	X	X	X	X	-	-	-	X	-	X
7	Tell Aswad II	Syria	7000-6500	-	X	X	-	X	-	-	X	-	X
8	Ghoraifé I	Syria	6700-6400	X	X	X	X	X	X	X	-	-	X
9	Halula- early	Syria	6700-	X	X	X	X	X	-	-	-	X	-

#	Site	Country	Date										
			6600										
10	D'jade	Syria	7600-7000	X	X	X	X	X	-	X	-	-	-
11	Çayönü	Turkey	7200-6700	-	X	X	X	X	X	X	-	X	-
12	Cafer Höyük	Turkey	7200-6200	X	X	X	X	X	-	X	-	-	X
13	Asikli Höyük	Turkey	6900-6500	X	X	X	X	X	-	-	-	-	-
14	Can Hasan III	Turkey	6600	X	X	X	X	-	-	-	-	-	X
15	Hacilar - early	Turkey	6700	X	X	X	-	-	-	-	-	-	-
16	Gritille	Turkey	6700-6600	X	X	X	X	X?	-	X	-	-	X
17	Ganj Darah	Iran	7300-6600	X	X	X	-	X	-	-	-	X	-
18	Abdul Hosein	Iran	7000-6000	-	X	X	-	-	-	-	-	-	-
19	AN Kosh, Bus Mordeh	Iran	7000-6600	X	X	X	-	-	-	-	-	X	-
20	Nemrik	Iraq	7500	-	-	X	-	-	-	-	-	X	X
21	Magzalia	Iraq	7500-6000	-	X	X	-	-	-	-	-	X	-
Fig. 4	**Late PPNB/PPNC (6500-5500 bc)**												
1	Wadi Fidan A	Levant	6500-6000	X	X	-	-	-	-	-	-	-	X
1	Wadi Fidan C	Levant	6000	X	X	X	-	-	-	-	-	-	-
2	Wadi el-Jilat 13	Levant	5900-5800	X	X	X	-	-	-	-	-	-	X
3	Azraq 31	Levant	6500-6000	-	X	-	-	-	-	-	-	-	X
4	Dhuweila - stage I	Levant	6300-6100	X	-	-	-	-	-	-	-	-	X
5	Ramad I	Syria	6200-6000	X	X	X	X	X	-	-	-	X	-
5	Ramad II	Syria	5900-5800	X	X	X	-	X	X	X	-	X	-
6	Ghoraifé II	Syria	6100	X	X	-	X	X	-	X	-	X	-
7	Tell Ras Shamra V	Syria	6500-5300	-	X	X	-	X	-	X	-	X	-
8	El Kowm I-A	Syria	6300-6100	-	X	-	-	X	-	-	-	-	-
8	El Kowm II-Caracol	Syria	5800-5700	-	X	-	-	-	-	-	-	X	X
9	Tell Bouqras	Syria	6300-5800	X	X	X	-	X	-	-	-	-	-
10	Abu Hureyra	Syria	6200-5900	X	X	X	X	X	-	-	X	-	X
11	Halula - late	Syria	6600-6000	X	X	X	X	X	-	-	-	-	-
12	Çatal Höyük	Turkey	5800-5600	-	X	X	-	X	-	X	-	X	-
13	Erbaba	Turkey	5800-5400	X	X	X	X	X	-	-	-	-	-
14	Jarmo	Iraq	6500-	X	X	X	-	X	-	X	-	-	-

			5500										
15	Ali Kosh, Mohammed Jaffar	Iran	5900	X	X	X	-	-	-	-	-	X	-

† Site numbers are shown on figures: Map 1 - Fig. 1, Map 2 = Fig. 2, Map 3 = Fig. 3, Map 4 = Fig. 4.

‡ All dates have been approximated to the nearest century.

Further, Hillman (1996) has highlighted the action superimposed on the climate after 16,000 bc of the Milankovitch effect, which is thought to have stimulated increased seasonality, with colder, wetter winters and hotter, drier summers. These conditions are thought to have been associated with increased fluctuations in rainfall and drought (Byrne 1987), which are said to favor the survival of plants with underground storage organs and species of annual habit (Blumler 1996). These include many wild legumes and grasses, such as the wild barleys (Hillman 1996).

Against this background, the following archaeobotanical data are outlined.

Archaeobotanical data from Southwest Asia between 17,000 and 5500 bc, with emphasis upon the grain legumes

The radiocarbon dates are those given in the original site reports, supplemented by more recent dates listed by Kuijt and Bar-Yosef (1994) and Kozlowski (1994), converted to bc. The data are considered in four time periods (Table 1): up to the end of the Epipalaeolithic, and then separately the three following millennia, during which there appears a developmental sequence toward the emergence of widespread cultivation.

The Epipalaeolithic: 17,000-8500 bc

For the Epipalaeolithic period, no new site data have been added recently. From the first, legumes and cereals are found in association (Table 1). Unusually, at Hayonim (Fig. 1) the pulse remains have been identified as the seeds of lupin, *Lupinus pilosus* Murray (Hopf and Bar-Yosef 1987). Abu Hureyra in Syria spans the forested period of the Interstadial and the Younger Dryas. The archaeobotanical remains indicate a reduction in the wild plant food base during the latter period, and within this, the grasses seem to be the most resistant to the effects of the harsh climate. An important development is the report of the early domestication of rye. This interpretation has been based on the presence of rye grains of morphologically domestic-type dating from about 8900 bc, and associated with the remains of a segetal weed flora (Hillman in Moore *et al.* 1998). Here too, a marked increase in lentil, *Lens culinaris* Medik., dating from a later phase toward the end of the Younger Dryas, is thought perhaps to indicate the onset of its cultivation, stimulated by the reduction in the availability of wild legumes in the area of Abu Hureyra during that period. It is thought that cultivation might have required seed obtained from other areas (Hillman 1996). Interestingly, legumes in general seem to have been important resources throughout all phases at Abu Hureyra, and during periods when evidence of pulse exploitation is slender, the volumes of small-seeded legumes, such as the members of the Trifolieae tribe, rise (Moore *et al.* 1998). However their role as potential food resources is speculative (Butler 1995).

Pre-Pottery Neolithic A (PPNA): 8500-7500 bc

During the subsequent millennium, at the end of the Younger Dryas and during the following period of climatic amelioration, increased early signs of cereal cultivation occur (Table 1), with domesticated barley and hulled wheat found at Jericho (Hopf 1983) and Iraq-el-Dubb (Colledge 1994a, 1994b) in the Levant and Tell Aswad in Syria (van Zeist and Bakker-Heeres 1982). All of these sites lie close to the forested zone, where pockets of grassland vegetation are thought to have survived (Fig. 2). Pulses occur on all these sites, even in those regions in Turkey and Syria which are thought to have largely been within zones of steppe-type vegetation. Bitter vetch, *Vicia ervilia* (L) Willd., seems to have been commonly exploited, and the Syrian sites have remains of pea, *Pisum sativum* L. From Iraq el-Dubb faba bean, *Vicia faba* L., has been identified (Colledge 1994b), a plant only known as a domesticate and whose progenitor is still unknown.

Fig. 1. Archaeological sites in Southwest Asia, site map 1, 17,000-8500 bc, modified from Aurenche *et al.* 1981. Refer to Table 1 for key to site numbers.

Fig. 2. Archaeological sites in Southwest Asia, site map 2, 8500-7500 bc, modified from Aurenche *et al.* 1981. Refer to Table 1 for key to site numbers.

Pre-Pottery Neolithic B (PPNB): 7500-6500 bc

This period is associated with the wetter, warmer climate toward the Holocene, a time of forest expansion. Domesticated cereals have been recovered from most sites (Table 1), and this development has been used to signal the beginnings of widespread cultivation of the associated legumes. Bitter vetch and pea are prevalent, and grasspea, *Lathyrus sativus* L., has been identified from sites in both Turkey and Syria (Fig. 3). This period sees the first appearance of chickpea, *Cicer* L. The sites of Beidha (Helbaek 1996; Colledge 1994b), Wadi el-Jilat (Colledge 1994b) and Ali Kosh (Helbaek 1969; van Zeist *et al.* 1984) all lie within a zone postulated to have a steppe or desert-steppe vegetation, yet all have yielded cereal grains and pulses. Ali Kosh also has high concentrations of small-seeded legumes during this time. Relatively large volumes of grain legumes have been recovered from Ain Ghazal (Donaldson 1985) and Yiftah-el (Garfinkel *et al.* 1988; Kislev 1985) in the Levant and Çayönü (van Zeist and de Roller 1991/1992) and Cafer Höyük in Turkey (de Moulins 1997). At Yiftah-el the circumstantial evidence for the cultivation of lentil is strong, as a particularly large volume of lentils was recovered together with the seeds of bedstraw, *Galium* L., a plant commonly found as a weed of lentil cultivation (Garfinkel *et al.* 1988). Furthermore, this site also contained a large number of the seeds of faba bean (Kislev 1985). Remains of this food plant also have been found at Ain Ghazal (Donaldson 1985) and a closely related wild vetch, *Vicia narbonensis* L., has been identified at Jericho (Hopf 1983). At this stage the first unequivocal sign of domestication in the pulses can be seen: the smooth-coated cultivated pea has been identified at Çayönü (van Zeist and de Roller 1991/1992) and Haçilar (Helbaek 1970), although at both sites the rough-coated wild subspecies predominated.

Late Pre-Pottery Neolithic B (Late PPNB): 6600-5500 bc

Toward the end of the Pre-Pottery Neolithic is seen the rise of the free-threshing wheats. This is associated with a decline in bitter vetch and pea, while chickpea has been found only at Ghoraifé (van Zeist and Bakker-Heeres 1982) and the pulse remains are predominantly lentil (Table 1, Fig. 4). From both Çatal Höyük (Helbaek 1970) and Bouqras (van Zeist and Waterbolk-van-Rooijen 1985) pea has been recovered, which has the smooth seed coat characteristic of the cultigen.

Summary of the archaeobotany and evidence for legume cultivation

From the Epipalaeolithic onward, pulses have been recovered at virtually every site which has yielded the remains of cereals. Lentil appears to have survived and to have been exploited throughout all periods, even when the vegetation is likely to have been highly restricted. It is important to note that within most plant assemblages there are also records of the remains of legumes, unidentified above the level of the genus *Vicia* or recorded just as pulses.

Fig. 3. Archaeological sites in Southwest Asia, site map 3, 7500-6500 bc, modified from Aurenche *et al.* 1981. Refer to Table 1 for key to site numbers.

Fig. 4. Archaeological sites in Southwest Asia, site map 4, 6500-5500 bc, modified from Aurenche *et al.* 1981. Refer to Table 1 for key to site numbers.

The early appearance of faba bean is hard to explain as so little is known about its ancestry; but as it is only known as a domesticate, then from current knowledge one must assume that its presence signals cultivation. The change from the rough to the smooth seed coat in pea is perhaps the most definite sign of a domesticated pulse, but this occurs only in that cultigen.

Most usually the only indication of legume cultivation is circumstantial evidence, and it has been shown above that all the following examples of this have been employed by archaeobotanists working with early Southwest Asian plant assemblages. Perhaps the strongest example is the association of legumes with the chaff of domesticated cereals, which itself carries recognizable morphological indicators. This assumes the synchronous development and practice of cultivation of cereals and legumes. The recovery of food plants together with seeds familiar as weeds of cultivation in the present is also used as evidence of cultivation (Willcox 1996; Hillman, in preparation); this assumes that associations of certain plant types are unchanging. New statistical studies appear to support this type of evidence (see Colledge, this volume). Large volumes of seed are sometimes thought to be unlikely products of gathering and thus are commonly held to be crops. This also might appear to be an unsafe assumption. However, the presence of a number of these conditions together would strengthen an argument for cultivation, as at the site of Yiftah-el.

Which environmental conditions can be tolerated by pulses?
What habitats and plant associations are most favorable?

The members of the vetch and chickpea tribes (Vicieae and Cicerae), from which the pulse cultigens were developed, all have distributions centered in the Mediterranean and Irano-Turanian regions (Kupicha 1981). The wild species, including the progenitors of the cultigens, are mainly relatively small-seeded, slender and tendrillous

climbers (Hardwick 1988). Characteristically they are found on shallow soils, on rocky hillsides and scree slopes, often in oak scrub and *Pinus brutia* woods (Davis 1970; Townsend and Guest 1974) and also in batha and steppe (Zohary 1972), and it appears that a wide range of soil pH and some salinity can be tolerated (Summerfield 1981). Bitter vetch is one species of a group of legumes, distinguished by a tendency toward an erect habit and a woodland habitat (Davis 1970; Townsend and Guest 1974). Plant distribution tends to be scattered in legumes, since the ripe fruits of wild species commonly disperse the seed for distances up to two meters (Ladizinsky 1987). This can be advantageous to taxa with light canopies, which tend to compete poorly. The current geographical distributions of the wild relatives of the cultivated grain legumes have been described and illustrated by Zohary (1996).

The grain legumes are adapted to withstand seasonal climatic fluctuations. They demonstrate a high degree of plasticity in environmental tolerances within populations. They have large seeds and hypogeal germination, said to be associated with a tolerance of relatively harsh climatic conditions. Hypogeal germination protects seedlings against frost and wind damage, insect damage and the effects of grazing (Summerfield 1981). Blumler (1996) has drawn attention to the observation that the annual habit and large seeds of crop plants favor survival under adverse conditions. An annual habit is found in all the known progenitors of the founder legume crops (Zohary 1996). Seed dormancy imposed by the impermeability of the seed coat is characteristic of wild legumes and retained to some extent in many pulse cultivars. This is a further trait favoring survival during and germination following periods of adverse climate (Blumler 1991).

Legumes are favored by the Mediterranean climate of hot dry summers, and mild wet winters (Nassib *et al.* 1988; Vavilov 1992). The two major environmental constraints to cultivated legumes are said to be unfavorable temperatures and lack of water (Buddenhagen and Richards 1988; Harris 1979).

Legumes tend to be strongly thermoperiodic; for example in pea the best growth seems to occur when diurnal temperatures fluctuate between 6 and 10°C. Optimally germination requires a temperature range between 10 and 30°C. Temperatures over 40°C tend to lead to pod loss, and high temperatures can be tolerated more readily when sufficient moisture is available (Saxena 1979; Saxena *et al.* 1988). Cold tolerance exists in a small generic range in each of the founder legume crops. Faba bean and lentil are the most cold-resistant, with field survival recorded down to -25°C in bean. Lentil is generally tolerant of temperature extremes (Summerfield 1981). Pea and chickpea tend to be less hardy. In general, plants that exhibit dormancy have the most cold-tolerance (Murray *et al.* 1988).

Generalizations can be made about the water requirements which vary with the species. Pea and faba bean need more water than chickpea, which has deep roots which allow it to withstand drier soil conditions. Lentil is also relatively drought-tolerant. Grasspea is best known for drought-tolerance, and also can survive waterlogging.

While these observations have largely been made on crop plants, it is likely that their wild relatives would display similar characteristics or even have a wider tolerance range. It is now known that many of the environmental constraints of the legumes are imposed by the associated nitrogen-fixing bacteria; for example, seed set can fail under drought stress owing to a decrease in nitrogen fixation by rhizobia (Pate 1977a; references cited in Stanforth *et al.* 1994), and nodulation is poor in plants in hot soils and may be reduced under conditions of high salinity (Sprent *et al.* 1988).

Given the wide intraspecific range of environmental tolerances and an apparent ability within populations to adapt, the grain legumes show particular advantages for survival during the major climatic changes following the end of the Pleistocene. It can be seen that they were available for collection by the human populations. Their representation within the archaeobotanical assemblages recovered from the earliest sites demonstrates that they were indeed recognized and utilized as food resources. Thus, that they were among the earliest cultigens is to be expected.

Certain of the cultigens appear to vary in their adaptability to certain environments, and this could add to our understanding of the distribution of the ancient pulse remains. That lentil exhibits a particularly wide range of tolerance, chickpea is least coldhardy and grasspea is most drought-tolerant may help explain their presence or absence at some sites during some periods. However, the absence of particular taxa among the archaeobotanical assemblages cannot be taken as an absolute absence there in antiquity, since post-depositional factors differentially affect preservation. The volume of any category of plant remains is also a feature of the use and distribution of the plant in antiquity and the fortuitous nature of the excavation plan. Consequently it is suggested that other than in exceptional circumstances, for example when the remains of a taxon are found in huge quantities, as at Yiftah-el, interpretations based on more than the record of a presence can be misleading.

Some nutritional aspects of the pulses

Pulses are well known for their nutritional properties, being high in carbohydrate and relatively high in protein

(Aykroyd and Doughty 1982:108). All contain some antinutritional factors. Lentil, pea and chickpea are usually considered easy to assimilate and to offer no dietary problems, but other pulses are less palatable or even toxic. Seeds of bitter vetch (and indeed lupin) contain alkaloids, and require leaching, while grasspea contains lathyrogens which ideally need leaching followed by roasting (Aykroyd and Doughty 1982). Their exploitation is perhaps hard to understand. Grasspea, as is noted above, is particularly well adapted to drought and can represent a ready and highly palatable source of food under famine conditions, as seen today. Bitter vetch, however, remains an enigma. This species appears to occupy woodland, so perhaps there were more forested conditions in those sites during the PPNB when bitter vetch was more readily exploited. This species is not known as a human food resource now, although it is an animal feed, but within the Hebrew text, The Mishnah (1993), for example, there are historical references to leaching the seeds for human food.

Problems in the archaeobotany of the pulses

The changes to the ancient seeds following charring in antiquity, and the taphonomic effects subsequent to incorporation within the site commonly complicate seed identification. Further problems inherent in the identification and interpretation of the fragmentary plant remains from very early sites have been described by Colledge (1991). Even in fresh material, the seeds of grain legumes characteristically do not show diagnostic morphologies and have proved difficult or impossible to separate beyond the level of genus or tribe. Most of the grain legumes which were taken into cultivation - lentil, bitter vetch, chickling or grasspea, and chickpea - can usually be identified by their gross morphology, but often cannot be separated from their wild progenitors or sometimes from close relatives (Butler 1990, 1992). The recognition of domestication in legume seeds is rarely possible in early plant assemblages (Butler 1989). Seed gigantism, a major sign of domestication (Smartt and Hymowitz 1985), is considered to be a relatively late development in the pulses, and has been said not to be observed convincingly prior to Roman times (Hopf 1986). Pea, alone within the Vicieae, portrays a micromorphological change from the rough seed coat of the wild subspecies to the smooth seed coat of the domesticate (Werker 1980/1981; Butler 1989), and faba bean is morphologically distinct, as stated above, and is without known close relatives.

Archaeobotanists commonly continue to measure legume seeds from early agrarian sites to seek signs of gigantism, as it often seems the only possible source of evidence of domestication. However a number of factors can affect the size of legume seeds.

Vavilov (1992:380-385) described in detail the trends in form and habit of crop plants that vary under the different environmental conditions found in various geographical regions. He noted that mild wet winters and hot dry summers are associated with low-growing, early maturing plants which tend to be indehiscent and have small seeds; wetter summer conditions extend the growing season, the plants are taller and seeds tend to be larger. Experimental observations in pulses have shown that high temperatures can promote taller growth, and that low temperatures can result in dwarfism with more tillering, a longer growth cycle and a higher pod yield (Pate 1977b). Colder climates appear to favor plants with small seeds: smaller seeds are known to germinate more readily than larger ones under cool conditions and are more drought-tolerant (Summerfield and Wien 1980; Summerfield 1981). However, under cool conditions and with the change to a low growth form, flowering in lentil is delayed and seeds tend to become larger (Summerfield 1981). The position of the fruit on the plant affects seed size: legumes are typically indeterminate and flowering proceeds acropetally. The pods produced at the lowest node mature first, and these have seeds which ripen first and are larger (Summerfield 1981). It has been noted (for example in wild lentils, *Lens culinaris* subsp. *orientalis, L. nigricans, L. odemensis, L. ervoides* and *Lathyrus blepharicarpus* L.), that commonly when a few nodes are bearing fruit, flowering may be inhibited until after the fruit mature. Then as a consequence, following any one harvest episode, the yield is of seeds at two or more states of maturity which may be of at least two sizes. It must be borne in mind that since these observations were made on only one or two populations of particular wild species, the results should be used only as cautionary examples.

Conclusions

In this paper the occurrence of the grain legumes on early sites in Southwest Asia has been updated with the most recent data, against an outline of a detailed model of the vegetational history during the major climatic changes following the end of the last glaciation. Some characteristics of the pulses have been described. These demonstrate that this plant group is well adapted for survival during harsh climatic conditions. While many other plant groups are likely to have succumbed to the climate, the legumes are more likely to have remained available as food resources and to have been taken into cultivation toward the end of the Younger Dryas. There are problems in the identification and interpretation of the remains of legumes from early sites.

The beginnings of legume cultivation are not discussed here. It is believed that the pathways to pulse domestication will have depended on their role in early human diet. This will form the subject of a subsequent publication.

Acknowledgments

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